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THE LIVING UNIVERSE

An Encyclopedia of
the Biological Sciences

The world of plants

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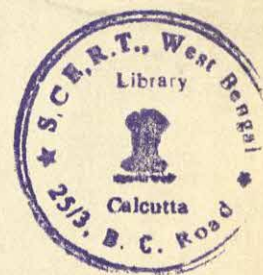
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The world of plants



THE LIVING UNIVERSE : AN ENCYCLOPEDIA OF THE BIOLOGICAL SCIENCES

THE LIVING UNIVERSE

An Encyclopaedia of the Biological Sciences

S.C.E.R.T., West Bengal

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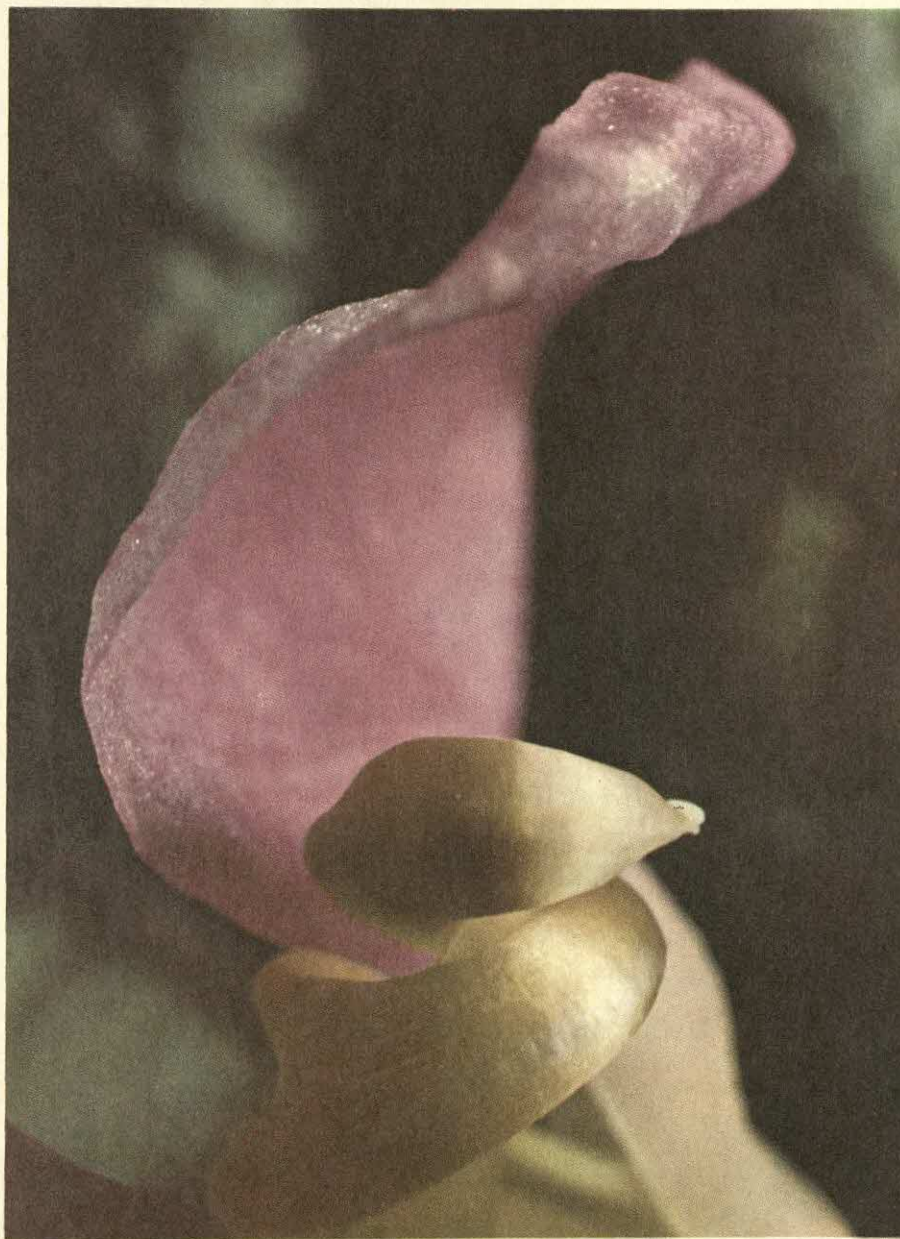
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The world of plants



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*A*NIMALS, of which man is among
the most dangerous, have established such a
hegemony over plants that these are generally

regarded as an inferior form of life. They are devoured, eradicated, and burnt without compunction in the ceaseless war that animals wage to keep themselves alive. Yet no animal would be alive at all were it not for plants which have harnessed sunlight to produce the organic compounds without which animals could not live. In addition, plants stabilize soil, conserve moisture, and preserve equable climate. Some of the most important problems in biological science have been investigated and solved on plant material. Finally, more gloriously arrayed than Solomon, plants fulfil man's striving after what he recognizes as beautiful things. There is no slum, however sordid, that would not be graced by trees in its streets. It is curious that there should be people who think that by restricting their diet to vegetables they are diminishing their debt to life. This book gives some of the reasons why the vegetable world is so worthy of interest, admiration, and respect.





THE LIVING UNIVERSE

An Encyclopaedia of the Biological Sciences

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The world of plants

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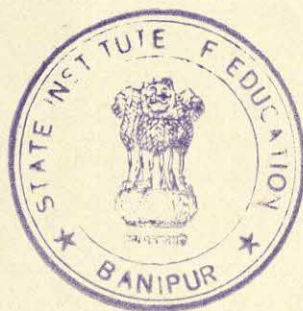
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Fig. 1. An example of plant cells taken from a green alga, Desmidea. Characteristic features are a cellulose material surrounding the cells, large vacuoles, and grains of chlorophyll. (Photo Lod).



Peculiarities of the plant world

Pierre CHOUARD



Plants have two main characteristic features. One is the function, that only plants possess, which makes all other forms of life dependent on them: this is the capacity to feed themselves, and grow, on the mineral world alone, without the help of any other living things. The other is a structural peculiarity—the formation of a membrane which closely envelops each plant cell. This anatomical feature may appear to be an unimportant device used for classification, but this is not the case. The two peculiarities of plant life are not unconnected, and all the other characteristics of plants, even the most striking, arise from them.

Plants constitute the only section of the living world possessing, in the majority of its representatives, autotrophic powers. In other words, they have the ability to make living matter with the help of energy drawn from the oxidation of reduced mineral substances capable of exothermic reactions (chemosynthesis) or with the aid of the radiant energy of light, normally provided by the sun (photosynthesis). Thus plants are the providers of energy-rich organic foods for

all other living things, animals and man.

In contrast to plants, animals are essentially heterotrophic, ie they must obtain all their energy-giving foods, in a complex form, already prepared by other living beings. Among plants, however, there are many degrees of autotrophy, from the most complete through partial or diminished forms down to its total absence.

An initial and continuous series of stages is in the loss of the degree of autotrophy for anatomical or physiological reasons, such as the distribution of functions among the organs of a single plant. For instance, the tomato plant as a whole is completely autotrophic, but its root grown in isolated culture is not. It must be supplied with sugar and even then it is unable to synthesize thiamine which has to be supplied to it like a vitamin. This loss of autotrophy is not permanent or genetically determined, and root-cuttings so often can give rise to completely autotrophic green plants.

Another series of stages leading towards heterotrophy is in the different species of 'vascular' plants, which may vary from semi-

(1) Degrees of parasitism: we can see a whole series of profound variations, of the nature of degradations, in the correlated structures of plant organs. We may, for example, quote mistletoe (a semi-parasite that is still green); dodder (a parasite without leaves and no longer green); bird's-nest orchid (a complete saprophyte), brownish in colour and almost completely without chlorophyll, its roots modified by association with fungi (mycorrhiza); down to plants that are completely parasitic, like the *Rafflesiaceae*, where both stems and roots are reduced to suckers, like the thallus of a fungus. Only the large and elaborate flower reveals the vegetable nature of this extraordinary organism.

(2) Relative mobility of plants and animals: there are some animals that are stationary like plants, and some plants that move about or move parts of themselves, like the sensitive plant; and there are animals with cellulose-like skins, such as the sea-squirt, and plants, temporarily without cellular membranes, that move about in amoeboid fashion, such as the plasmodia of the group of fungi called *Myxomycetes*.

(3) Tropisms: zoologists use this term for the movements of whole organisms, which botanists call 'tactisms'.

(4) Gastrulation in animals: the types of gastrulation vary considerably from the primitive pattern, and this is not the place to describe them in detail. But it is a peculiar and fundamental property of animals. As a result, the cells of the gastrula, although they are all descended from the same egg-cell, are exposed to conditions and positions that vary greatly according to whether they are inside or outside, near the mouth or at the bottom of the sac, and these factors control their further differentiation. An intermediate layer of cells, the mesoderm, is formed. This in due course constitutes the general body-cavity, or coelom, where various organs will eventually develop. Various processes of folding and delamination can yield results analogous to those obtained by invagination.

(5) Plant carbohydrates: these include the whole range of hexoses, pentoses, heptoses, etc., singly or in combination; remarkable polyhydric alcohols, particularly in the algae and fungi; starch in all its varieties (replacing glycogen, except in the yeasts); inulin and the whole family of fructoses, galactoses, and mannoses, etc., up to cellulose and the various forms of pectin.

(6) Phenol compounds and their derivatives or associates: these also include the whole family of tannins and their compounds, the miscellaneous and varied group of heterosides (which includes the principles of mustard and of bitter almonds), and most important of all, the wide range of water-soluble pigments that give their colours to flowers, young leaves and dead leaves, that is to say the group of anthocyanin pigments that make the plant world so attractive.

parasitism to complete parasitism¹ or to saprophytism, ie nourishment on organic matter derived from decayed living things, such as the humus formed from dead leaves.

Above all, it is in this ability to synthesize, to a greater or lesser extent, various essential complex molecules out of the common supplies of carbon materials, nitrogen and sulphur compounds, that certain groups of plants differ from one species to another, and from race to race, because of equivalent variety in their inherited constitution. Fungi, especially, exhibit a complete range of races which differ according to their needs for vitamins.

It is a time-honoured distinction between the plant and animal worlds that of all living things the former are immobile² and clothed in cellulose membranes, and the first of these characteristics is consequent on the second. In this crude form, this is not a satisfactory definition of plants, and we must take a broader and closer view so as not to consider these properties to the exclusion of the other peculiarities of plant life already noted.

Plants with the power of autotrophy utilize the energy that results from it to manufacture first and foremost the substances known as carbohydrates, ie sugars and their derivatives; and these products are soon present in excess. Cellulose and related compounds belong to the group of carbohydrates which are the constant products of photo- and chemosynthesis; and although it is not absolutely essential for the production of living matter to be associated with the formation of cellulose, this membrane formation avoids the clogging of the cell by an excess of soluble carbohydrates and so favours the prolonged functioning of chemo- and photosynthetic processes. In fact, all autotrophic plants form insoluble membranes which are deposited, like excreta, at the margins of the cells. This property appears to be more fundamental to plant life in general than even the autotrophic processes, since the formation of cellular membranes is found in a modified but always discernible form even in the fungi, which are entirely heterotrophic though obviously derived from autotrophic plants.

The membranes are flexible but inextensible when growth has ceased, and consequently plants in general are more or less fixed in one place. In particular, they have no muscles, which are a characteristic of animals. But the immobility of plants is only apparent. Once they have acquired their membranes, plants cannot carry out even the simplest animal or amoeboid movements, which are a

sort of creeping of the protoplasm; but within the confines of the membrane, cytoplasmic mobility persists as shown in the stirring circulation ('cyclosis') of the protoplasm, which reveals evidence of active cellular life. It is also seen in plant cells temporarily without membranes, like those of the plasmodia of Myxomycetes.

Unicellular plants, or those consisting of masses of poorly differentiated cells, often move about in water by the action of flagella. These movements, which are common to plants and animals, can be directed by external factors, and are known as tactisms.

Multicellular and more highly differentiated plants are usually fixed, and subject only to passive movements induced by currents or winds. However, we must not forget certain important plant movements, such as those of growth. Young tissues grow and bear the flowers which distinguish the plant in a different place each year; after every spring, lily-of-the-valley root-stocks, iris roots, hyacinth bulbs, oak twigs and bamboo stems advance their growing points. In exceptional cases these growth movements are so vigorous as to be visible to the naked eye after the space of a few minutes. They are influenced in direction by certain environmental factors such as light and gravity; the young plant organs bend, and their bending movements are called tropisms by botanists.³ Some of them are intrinsic, such as the winding growth of tendrils and twining stems.

Other more rapid movements of certain plant organs are effected by alternate swelling and shrinkage of groups of cells more or less filled with water, which bring about so-called nastic movements, such as the folding and unfolding of clover leaves, the opening and closing of a tulip flower, and the rapid movements of the leaves and leaflets of the sensitive plant.

The immobility of plants is thus only an appearance, a sort of rough approximation. It hides many different kinds of movement, but none of them shows any tendency to evolve clearly in the directions of muscular contraction or control by a nervous system, which are solely animal features.

The plan of organization

Plant cells, at each division, weave a layer which partitions off the two separate protoplasts, so preventing them from parting. This leads to consequences which are fundamental for the plan of plant organization, giving it

an originality that is particularly distinct.

We know that during its embryonic life an animal develops by a process of gastrulation which is never found in plants. First there is a solid mass of cells (the morula), which then becomes a hollow sphere (blastula) by the splitting apart of the cells in the centre. Finally, one side of the blastula folds itself into this cavity like the finger of a glove turned inside out, so that the embryo now consists of two layers of cells in the form of a bag open at one end (the gastrula).⁴

Nothing like this is seen in plants. Embryonic cells never normally split apart; the embryo cannot pass beyond a stage equivalent to the morula, because plant cells have these characteristic rigid membranes which hold the daughter cells bound to each other, at least at first. In consequence, as the embryo grows it cannot enlarge in all directions, but only towards the periphery of the original sphere, and especially in two opposite directions, from the two poles of the axis originally determined since the formation of the egg by the entry of the male gamete, and the position of the embryo relative to its maternal coverings. The growth of a plant embryo is therefore linear and bipolar to begin with, and although it may later be complicated by the formation of layers or by secondary axes, it never takes the form of a hollow sphere folded back into itself.

It is therefore true to say that the essential structural difference between multicellular plants and animals is that the former are solid bodies, and the latter hollow. The enormous variety of anatomical patterns of animals arises from the many directions in which their cavities can fold and grow. The growth of plants, on the other hand, consists normally only of the extension of the ends of a straight axis, and of the thickening of this axis, and also of various kinds of expansion and lateral ramification.

In flowering plants, however, there is simultaneous double fertilization: the formation of a normal egg and of a supplementary egg made up of a male nucleus and a double female nucleus, which gives rise to an albumen-containing structure known as the endosperm. This at first usually forms no membranes, or only incomplete ones, so that its earliest cells become arranged in a kind of blastula which contains the true embryo. But the endosperm's function is only temporary; it is soon absorbed by the true embryo and disappears. Exceptionally, for example in the peony, it is the normal ovum that divides like a completely

hollow blastula; but the tendency of plants to form buds from solid organs is such a fundamental feature of plant embryology that this sort of blastula continues its development by later forming little embryos, of the normal solid plant type, which bud off at several points on its surface.

The structural patterns of plants are thus very much simpler than those of animals. On the other hand the plant has some unique properties. The two ends of its growth-axis, the shoot and the root extremities, both retain indefinitely the power to grow like the two ends of a young embryo, at least so long as flowering does not occur. The masses of young or embryonic cells, formed at each end in 'growing points', are known as 'primary meristems'. Until flowering eventually occurs, the growing point of a stem retains all the potentialities of an embryo, for it continues to maintain itself autotrophically while forming leaves and axillary buds; and if the base is cut away, it forms roots and a complete plant is remade. Axillary buds can do the same. A plant is not a clearly defined individual, for at any time it can divide into as many independent organisms as it possesses buds.

The growth of a plant, even of a big tree, with all its roots and branches, is thus a kind of continuous embryogenesis. It does not really resemble the fully-grown state of an animal at all. The differentiation of plant tissues does not greatly alter their development potentialities in general. By providing isolated organs or tissues with adequate nourishment, it is often possible to induce their cells, sometimes even a single cell, arising from any organ or tissue whatever, to redifferentiate and reorganize themselves first into a bud, and then into a complete plant.

In most animals, on the other hand, and in all vertebrates, the adult state is preceded by the complete separation of the purely reproductive tissues which will form the generative organs, and the tissues of the body, which will form all the other organs. Such a separation in plants is never final, because any tissue, whether the skin of a leaf, or even a stamen or an ovary can be redifferentiated under certain conditions, and re-form a complete plant with roots, buds, leaves and flowers.

In the same way, experimental teratogenesis, the deliberate production of monstrosities, must be associated in animals with embryogenesis and cannot be extended into adult life. In plants on the other hand, experimental teratogenesis is possible with any organ throughout its life.



Fig. 2. Dodder, a flowering plant related to the convolvuli, is incapable of living independently and autotrophically. Here is a young *Guscuta Gronovii* that has germinated at the foot of the spotted green stem of a *Xanthium*: it inserts its suckers into the stem of its host, whilst at the same time the primitive root disappears. The parasite's tissues are yellowish-white, but look greenish in the picture, because of the reflection of the green colour of the host. (Photo Lod).



(a) The seeds of *Odontoglossum* are very fine, and a gram of them contains more than a million. Each seed consists of only a small number of cells ($\times 35$).



(b) After disinfection with calcium hypochlorite, the seeds are sown aseptically in a test-tube. After about two months, they have grown into little green masses called 'protocorms'.



(c) Protocorms magnified. The background millimetre-squared paper shows the scale.



(d) A young plant removed from the culture-tube about five months after sowing, ready to be planted out in a pot on osmund fibres.

(e) Young *Odontoglossum* plants on osmund fibres.





(f) 6-7 years after sowing, the plant produces its first flowers. (Photo Lod).

The birth of an orchid

Fig. 3. The germination of exotic orchids was a mystery to botanists for a long time. It was at first thought that the assistance of symbiotic fungi which occur under natural conditions, was essential (Noel Bernard). However, Knudson showed that it is possible to grow orchids under sterile conditions, on synthetic media which replace the action of the symbiotic fungi. This series of photographs illustrates the development from seed to flower of an *Odontoglossum*.

Biochemical peculiarities

At first approach the biochemical composition of animals and plants is fundamentally the same; it consists of systems of protein macromolecules shaped by the effects of nucleic acid macromolecules with genetic and physiological properties, and of the resulting enzymes. However, if a list of the direct principles of plants is drawn up, one finds an enormous number of substances, varying greatly in structure and function, most of which are peculiar to the vegetable kingdom. Many more are still to be discovered.

In relation to autotrophy (or its chemical consequences), the 'biochemical factory' of plant life is indeed powerful, rich and varied. Without giving a complete list of its products, perhaps we may select a few for brief description.

First are the pigments used in photosynthesis: chlorophyll and its analogues. Carbohydrates, after passing through short intermediate stages, are among the first products of photosynthesis. Plants also are remarkable for the extraordinary diversity among their carbohydrate groups and analogues.⁵ Plants also exhibit a rich variety of lipids, or fats, particularly oils, glycerides, waxes, sterols, etc.

There is often an association between the plants' richness in sugars and a number of phenolic and polyphenolic compounds of varying complexity, which may be joined to each other and to carbohydrates.⁶

At the meeting point between these chemical groups are found the constituents of lignin, which is the basis of wood, and of suberin, the ground-substance of cork, two of the fundamental materials synthesized by the plant factory.

In addition to all these products, there is a kind of chemistry, whose ultimate purpose is not apparent, but which is evidence of the great versatility of the machine built up on the basic process of photosynthesis. Examples of these products are water-soluble pigments, which plants seem to waste in their flowers, fat-soluble pigments of the carotinoid group, derivatives of isoprene, and the ill-defined range of alkaloids, those basic nitrogenous compounds that are almost superfluous in the plant economy but act powerfully on the nervous systems of animals.⁷

Plants differ from animals also in their stimulatory and inhibitory substances, for plants synthesize their own hormones for the

growth of cells enclosed in their membranes, for the growth of the membranes themselves, linked with their extensibility when young, and for cellular multiplication. These hormones have only recently been isolated and are one of the main centres of interest in plant physiology today. They include the auxins, gibberellins, kinetin and kinins, whose activity is so great that it is disclosed in quantities of the order of one ten-thousand-millionth of a gram.

Cellular peculiarities

Whilst membrane-formation is characteristic of plants, vacuoles⁸ are hardly less important. They appear only in young cells with dense cytoplasm, from rudiments formed by very hygroscopic proteins; these grow as the cell itself grows and differentiates, becoming liquid drops consisting mostly of water in which colloids are diluted and other substances are dissolved.

Vacuoles play an essential part in plant life. By virtue of their more or less concentrated solutions, and the membranes of varying degrees of semi-permeability that separate them from surrounding media, they make possible the process of osmosis,⁹ which is carried on by all living cells, but particularly those of plants.

The plant cell, generally adapted as it is for actual or potential photosynthesis, exhibits a remarkable apparatus of plastids, ie lipoprotein inclusions which are related to mitochondria, but adapted to assist in the performance of various complicated functions. Chloroplasts are the most astonishing apparatus of the plant cell. The electron microscope has revealed their lamellar structure, which is very complex and fundamental to their photosynthetic function. Together with the nucleic acids and the chromosomes, which carry the hereditary factors, they furnish the finest examples of biochemical mechanisms depending on structural complexity, which would be utterly improbable in a homogeneous mixture with the molecules scattered about.

The nuclei of plant cells present a considerable number of both general and specific peculiarities, and one of them makes plants of unique interest in the study of heredity. This is the ease with which the nucleus can remain active and in harmony with its cytoplasm, while losing half the normal diploid number of its chromosomes, thus attaining the haploid state; or when the number is multiplied (polyploid state); or even if it gains or loses



Fig. 4. An extreme example of natural propagation by a shoot: the leaves of *Scilla ledienii* (a plant from the Congo) re-form a tiny bulb at their tip, complete with roots and leaves.



Fig. 5. Ferns (this picture shows *Osmunda cinnamomea*) exhibit the cycle of haploidy-diploidy in two kinds of individual which alternate regularly. Spores of this form develop into little dark green strips, the prothalli. These are haploid and produce the gametes, the agents of fertilization. From these arise fertilized eggs which yield the diploid generation of leafy fern plants. (Culture prepared by M. G. Morel, I.N.R.A., Versailles. Photo Lod).

one or more chromosomes (aneuploid state). These phenomena, although relatively rare in animals, are quite common in plants, sometimes even in the same plant, and are fairly easy to induce, either by hybridization, by chemical treatment (eg with colchicine or various mutagenic substances) or by physical agents (ionizing radiations, X-rays, gamma-rays, neutrons, etc). Thanks to the use of plants exhibiting polyploidy and its variants, our knowledge of the laws of heredity is constantly increasing.

Biological peculiarities

Some features of plants are equally peculiar but of a more complex nature, and have implications for biology as a whole. They also distinguish plant biology from that of animals.

We know that in animals the line of diploid¹⁰ cells that will make up the entire body from the embryo to adult life is started at the time of fertilization. Certain groups of cells of the reproductive glands only will undergo chromatic reduction (or meiosis), giving short successions of lines of haploid¹¹ cells from which ova and spermatozoa result. It is much the same in flowering plants, which are entirely diploid, and in which only the lines of pollen cells and embryo sacs constitute the haploid phase.

In the chapter contributed by Professor Maresquelle we shall see a general account of these variations. Suffice it here to say that among plants there are some that are always haploid, where fertilization is immediately followed by meiosis with return to the haploid state; there are others in which the two phases, haploid and diploid, are of similar or even equal duration; and others again in which the diploid state predominates just as in animals, as we have seen among flowering plants. In comparative biology this is known as the 'alternation of generations'.

The different kinds of polyploidy and the varieties of alternation of generation meet and combine simultaneously in plants, thus providing valuable opportunities for research and discovery in the fields of heredity and physiological genetics.

Plants also behave peculiarly in their division into sexes, whereas we know that separation of the sexes in different individuals is a rule with few exceptions among animals. In conjunction with their constant diploidy, this situation offers only one sort of experimental possibility for the analysis of sexual



differentiation. Plants, on the other hand, are much richer in this respect; hermaphroditism is the general rule in flowering plants, and the separation of the sexes, although less common, is nevertheless not rare, as in the monoecious state (flowers of different sexes on the same plant) or the dioecious state (different sexes on separate plants). If we review the whole of the vegetable kingdom, we find these different degrees of separation of the sexes in combination with the various kinds of alternation of generations;¹² the biology of sex can be analyzed completely only by a study of the whole plant world.

Normally, we consider that, to a greater or less degree, sex results from a difference in genetic constitution, which, completed by fertilization, ensures the viability of the normally diploid organism. In plants genetic differences of another kind may be involved, as shown by the degree of ease with which fusion can occur between two different lines, and the reluctance to join of two individuals of the same line. Fungi, and particularly the Coprini, with their four sexes, illustrate the principle of these different kinds of sexual organization (see 'Flowerless plants').

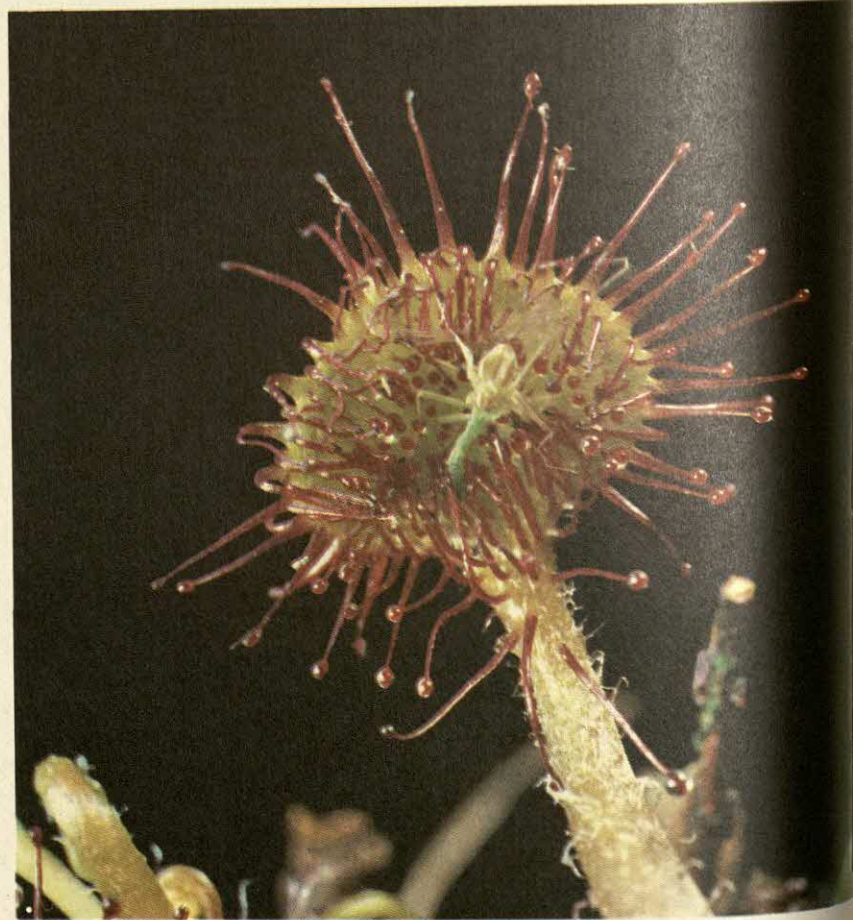
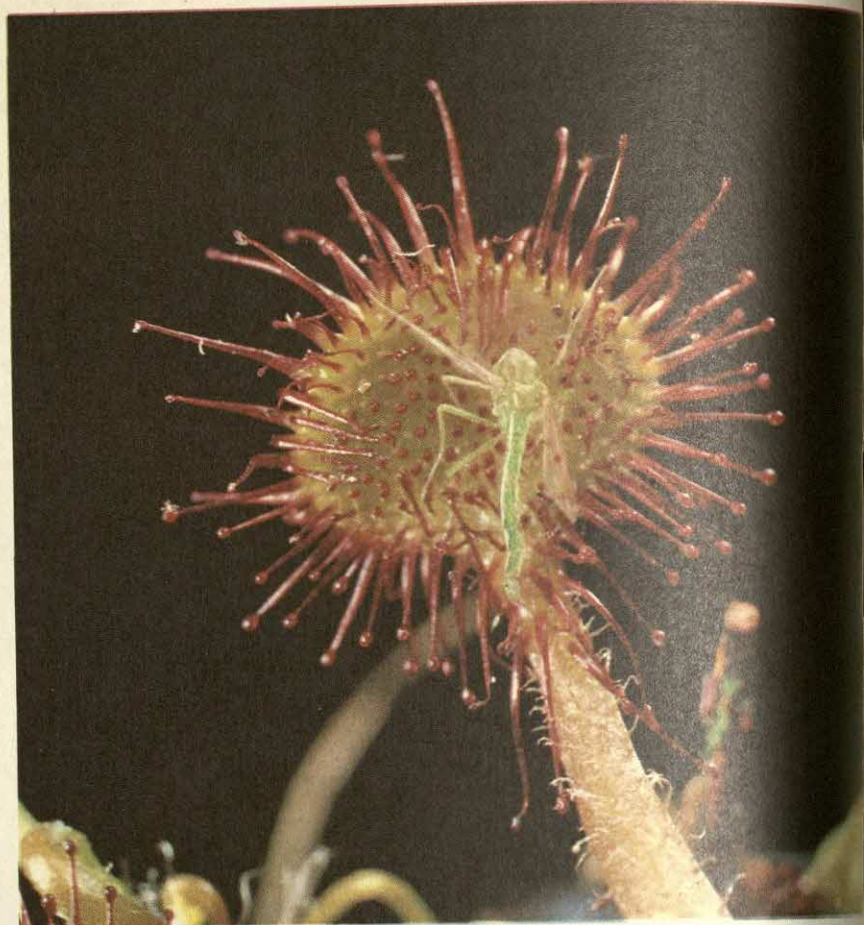
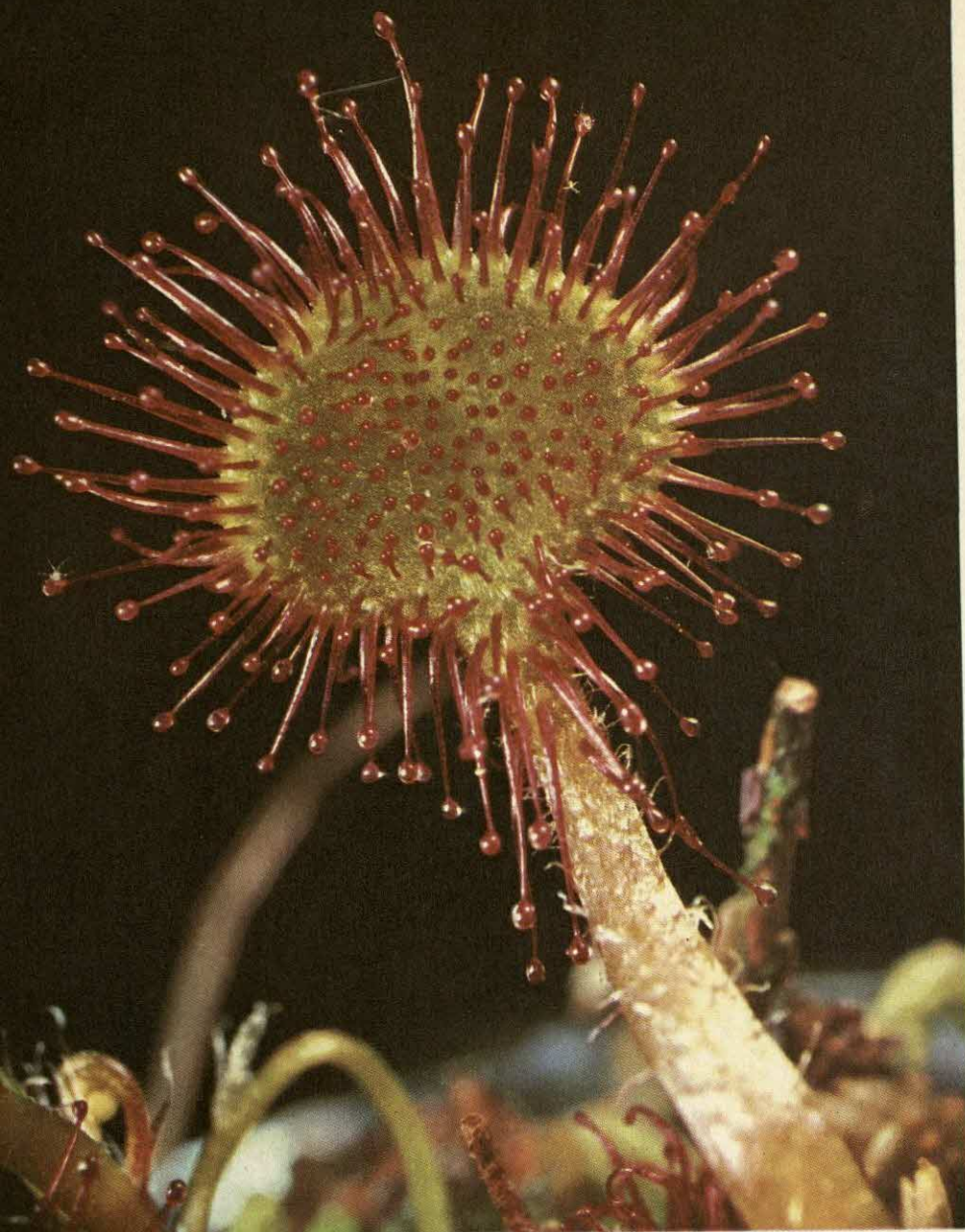
The superimposition, or substitution of two entirely different types of sexual segregation, leads to the same result, namely the mingling of two parental genetic inheritances, which usually enhances the vigour of their descendants. This is one of the unique features of the plant world.

Finally, the processes of multiplication

Fig. 6. The two sexes, usually close together in the same flower, may be more widely separated: here, in the chestnut, the same branch bears male flowers in the form of long catkins with stamens, while the female sex is represented by groups of flowers with ovaries and long styles which give rise to the fruits (chestnuts) contained in the same spiny husk. (Photo Lod).

(7) Carotinoids and derivatives of isoprene: the former comprise the colouring matter of carrots and the xanthophylls of etiolated leaves and ripe fruit. Closely related to the phytol of chlorophyll itself, they are also connected with the huge family of gums like rubber and other derivatives of isoprene, and with essential oils and resins with heterocyclic nuclei, which give plants their scents.

(8) Vacuoles may become very large, and occupy nearly all the interior of the cell, leaving only a thin layer of cytoplasm against the cell membrane, and a few strands in between. During metabolic crises, they may break up temporarily into many small drops, which later coalesce to re-form large vacuoles. When a cell de-differentiates and returns to the young or almost embryonic state, its vacuoles may regress.



Sundew, a carnivorous plant

Just as animals could not exist without feeding on plants, there are plants that take their revenge by devouring animals. These so-called carnivorous plants actually supplement their normal nutrition by photosynthesis with the assimilation of organic matter from animals. Above: the round-leaved Sun-dew, which is found in peaty marshes, has glandular hairs on its leaves, all of which are insect-traps. These secrete drops of sticky material, like the gum of a fly-paper. Top right: when an insect is caught in the trap, the hairs bend inwards on to the prey, which is ensnared in the viscous secretion that is also capable of digesting its tissues. Bottom right: the prey is completely stuck down and will be wholly digested and absorbed by the leaf. The trap will then open in a new condition of readiness.

which avoid sexual reproduction are no less remarkable in plants. Examples of their enormous ability to reproduce vegetatively are cuttings, layers, division, grafting, parthenogenesis, apogamy, apospory, and polyembryony. All these phenomena are seen in plants, but some of them are rare or non-existent in the majority of animals.

Many more examples of the peculiarities of plants could be given, but we shall conclude with one more, which is the importance of the phenomena of physiological periodicity, or what is sometimes called 'biological time-keeping'.

Plants possess a mechanism for keeping count of the passage of time, so that they can ensure the continuation of cyclical phenomena, which may or may not be linked with natural rhythms. The daily and seasonal variations in illumination to which plants are exposed at different latitudes influence them profoundly, through photosynthesis. Because of their immobility, plants cannot escape from the extreme variations of temperature between day and night, summer and winter. Some are fixed on the sea-shore and exposed to the rhythm of the tides. It is therefore not surprising that the whole of the plant kingdom, much more than the animal kingdom, shows clear-cut types of photo- and thermoperiodicity attuned to diurnal, seasonal, or even lunar rhythms. In the case of photoperiodicity, it is becoming clear that light acts by its influence on a pigment which is probably universal, whose colour changes from light red to dark red and back, and which also plays a part in many other phenomena. The various rhythms and their mechanisms present physiology with one of its most urgent problems. These remarkable facts, which are further elaborated in later chapters of this volume, contribute a rich variety to the fields of general biology and physiology.

In the past, although plants, having neither shell nor bony skeleton, have left less than animals in the way of fossils, they have nevertheless played an important part in the formation of deposits. It is only because plants and bacteria produced coal and oil fields that man was able a few centuries ago to enter the industrial era. Although immense calcareous deposits arose from madrepores or planktonic animalcules, all this marine fauna must have fed directly or indirectly on the green plants of the oceanic plankton. Our atmosphere is relatively rich in oxygen because plants give it off during the day. It is they also that, by providing food for madrepores, enabled large

quantities of carbon to be fixed in the calcareous deposits, almost too completely, and thus relieved the primitive atmosphere of the excess of carbon dioxide it might have contained.

The geochemical activity of plants is still considerable at the present time: each year about 135 thousand million tons of carbon obtained from the gas carbon dioxide are fixed in the oceans, and about 10-16 thousand million tons on dry land, through the action of photosynthesis. If we take into account the fact that photosynthesis is partly balanced by respiration, there must be nearly 200 thousand million tons of carbon in the form of carbon dioxide returning to the plants of the world each year. The earth's atmosphere is estimated to contain carbon dioxide equivalent to 700 thousand million tons of carbon, and the oceans the equivalent of 30-50 billion tons, which keeps the level of carbon dioxide in the atmosphere constant.

Thus within the limits of these approximations we may say that every 250 years, all the carbon dioxide of the air and of the seas in the entire world is taken in by the plant kingdom, and set free again through the activity of bacteria and animals.

It can be shown that nowadays plants inhabit most regions of the world, with the exception of the most arid deserts and the polar ice-caps. The oceans are occupied by algae, on the shore and on the illuminated part of the submarine continental plateau; and planktonic algae are distributed throughout all the seas where any light reaches. Although in a very dilute form, this population of algae constitutes the greater part of the plant world, perhaps of the order of ten times the weight of all the plants on dry land.

The dry land is populated by an enormous variety of plants, ranging from lichens to savanna plants and forests. Only extremes of climate and very steep mountainsides prevent the growth of plants. Everywhere they grow, plants tend to protect the surface by turning the superficial rocks into a true soil, the basis of fertility in agriculture.

Although most plants inhabit the illuminated surface of the earth, the world of darkness is also partly occupied by plants. The undergrowth of forests, which is more or less dark, usually damp, and always rich in decomposing organic matter, is the place where fungi naturally develop. Provided water is available, wherever there is organic matter, even in total darkness, its progressive mineralization will always be effected by living things,



Fig. 7. Fungi are typical examples of the complexity in sexual pattern of certain plants: they are the only living organisms that have not two but four different sexes.

(9) *In direct or indirect contact with water, plant cells swell through the osmotic entry of an excess of water, until the stretching of the cell membrane exerts a pressure of turgidity equal to the osmotic pressure that arises from the difference in concentration between the solutions inside and outside the cell. Consequently, even when deprived of all supporting tissues, plants normally have a more or less firm and rigid consistency (like that of a fresh lettuce leaf); this consistency is due to the turgidity of all the cells that make up the plant. If this turgidity diminishes as a result of an osmotic loss of water contained in the vacuoles, the plant wilts; this is the usual mechanism of withering.*

(10) *ie with two sets of chromosomes: the condition called 'diploidy'.*

(11) *ie with a single set of chromosomes: this condition is called 'haploidy'.*

(12) *Combinations of patterns of separation of the sexes with that of the alternation of generations: there are cases where the differentiation of the sexes may spring from causes or mechanisms that are quite different. Sometimes separation of the sexes is even produced in the course of the diploid phase, sometimes during the haploid phase, or sometimes on the other hand as a direct consequence of meiosis or of fertilization. This means that the distinction between the sexes is found in different cases to be associated, or not, with positive but opposite nuclear events, or associated with the permanence of the same nuclear states linked in a greater way with physiological phenomena.*

especially by the action of bacteria and moulds.

After violent disturbances of the earth, such as volcanic eruptions, upheaval of mountains, and inroads by the sea, plants cover the new ground with a carpet which protects the surface from being washed away.

Finally, man spreads over the earth. All his primitive activities are closely connected with plant life: first the gathering of berries and the capture of herbivorous animals, and later the development of agriculture, either in its static form or by the nomadic exploitation of pasture lands by herds. Only a few centuries ago, nearly everything that man ate came directly or indirectly from plants, and cultivation, ie agriculture, was the only important source of the economy. Food came naturally from plants and from the animals that fed on them. Clothes, fibres and fabrics also came entirely from agriculture; and paints, varnishes and detergents had the same vegetable origin. Wood was essential for carpentry, and was also the source of heat. Domestic animals provided a means of transport.

Now, since the general exploitation of mineral wealth and the utilization of coal, the situation has changed radically. Products of the field have been increasingly replaced by those of the mine, first coal, then oil as sources of energy, and more recently for synthesis by the chemical industry; so that the provenance of detergents, plastic fibres and fabrics, fuels, and means of transport is nowadays industrial rather than agricultural. Only food remains the exclusive preserve of agriculture, and trees no longer needed for building and heating are used for wood-pulp.

It may be asked whether the importance of plants and of agriculture will not diminish still further. The reduction in the proportion of the population employed in agriculture, which in highly industrialized countries like the United States has fallen to about 10 per cent, might seem to indicate this. The final part of this volume will show that it is unlikely. Up to now, food has been synthesized only in insignificant amounts, and we shall have to rely on plants for complex therapeutic drugs for a long time to come. Furthermore, the growth of the population will necessitate increasing recourse to plants for food. Although nuclear power and electricity obtained from sunlight may satisfy our future needs for energy, it is inevitable that one day the coal mines and oil fields will be exhausted, and we shall have to return once more to plants as the raw materials for industry.

The plant world's capacity for production

is truly enormous, for it is based principally on the inexhaustible energy of the sun. We must measure the activity of plants in terms of energy; in this sense, we may say that the whole of plant life, wild and cultivated, forests and pastures, covering in the temperate zone a country of the size of France, makes a quantity of organic material equivalent to a layer of coal 0.1 mm thick covering the whole surface of the country in each year. Although extremely thin, this layer, owing to its area, represents an enormous weight—of the order of 70 million tons, for France. This is approximately equal to the annual consumption of coal, which is more than that extracted from all the mines of the country. And when the mines are exhausted, plant production will not cease, but will increase as fast as the progress of plant physiology and agricultural technique.

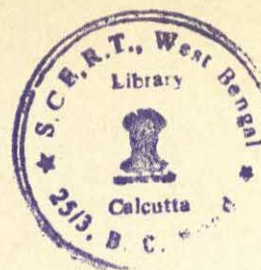
As a matter of fact, the energy radiated by the sun in the same period (about 1 kilowatt per square metre during daylight hours) is equivalent to a layer of coal nearly 10 cm thick, more than 100 times what is produced by the best harvests of cultivated plants during their productive season. There is thus considerable room for improvement in the efficiency with which plants utilize the sun's energy, and this margin opens up possibilities for great progress. The technical difficulties in the achievement of this progress are small compared with economic ones, particularly the slowness with which improved methods reach the great mass of farmers and peasants.

Man does not live by bread alone. The carpet of plants is not only a useful top-dressing, but also an adornment in which our eyes discern the beauty of the colour of flowers, of foliage, of the shape of trees harmoniously grouped; and the profound sense of belonging to the world of nature gives us the picture of fertility and stability. Plants are the ornaments of our gardens and our houses, as well as the indispensable adornment for our dinner table. They constitute elements of a setting which is all the more necessary as man lives increasingly in an environment of manufactured articles. Although it may be entirely subjective, this is one of the more important reasons for our interest in and our fondness for the plant world.

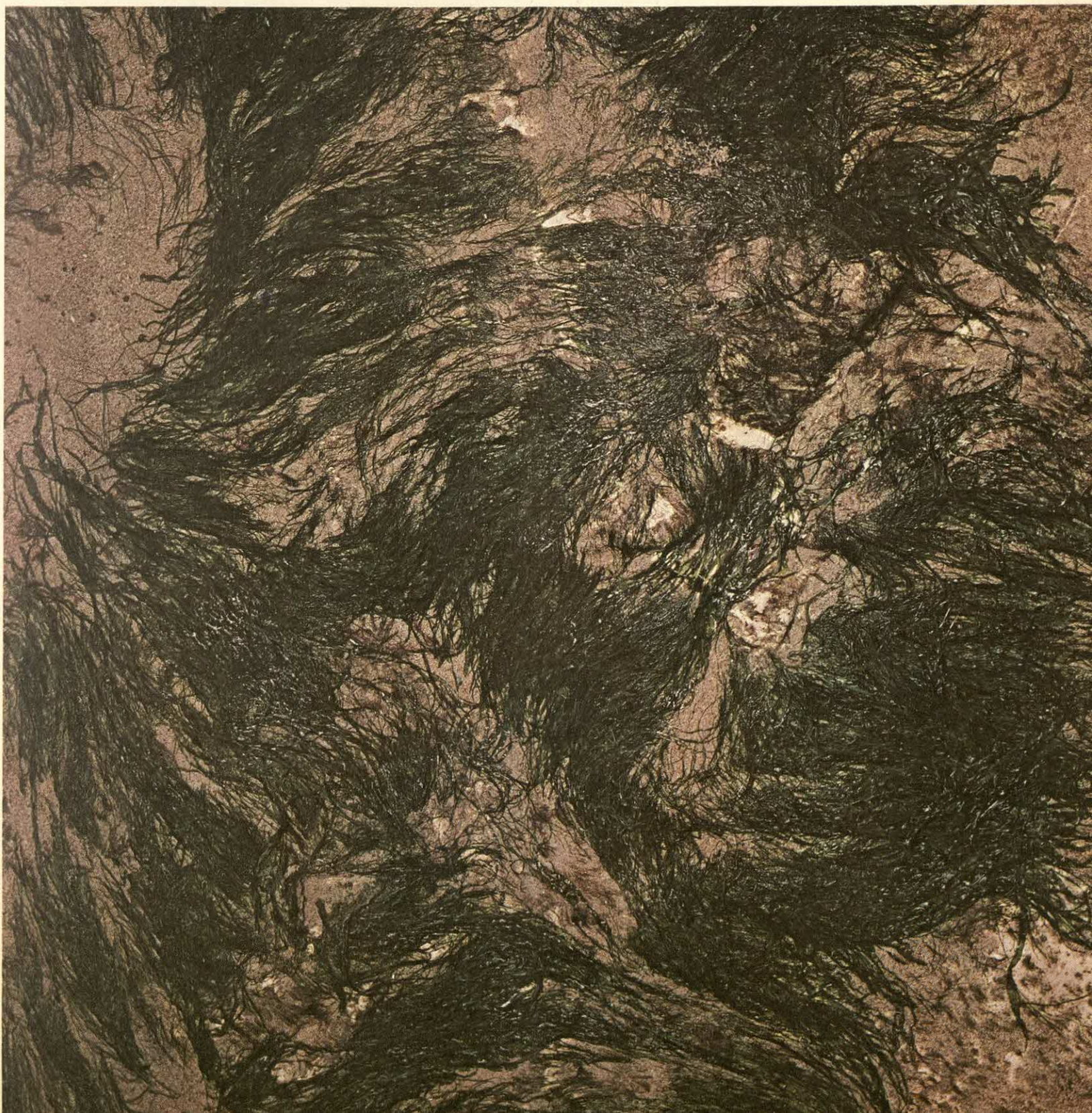
In the succeeding chapters of this book, examples will be given which will further bring out some of the peculiar characteristics of the plant world. The most striking ones have been summarized in the preceding pages.

PART ONE

S.C.E.R.T., West Bengal
Date 7-5-87
Acc. No. 4002



Colonization of the mineral world



*Plants
colonize the
mineral
world: algae
growing on the
rocks of the
sea-shore.
(Photo Lod).*

The plant as a photosynthetic factory

A. PIRSON and A. MOYSE

(1) Man is constantly looking for ways of harnessing the sun's energy directly, as in the present-day 'solar ovens'. The results are encouraging, though small in amount compared with those achieved by plants.

(2) 'Light quanta' or 'photons' act at molecular level.

(3) Polymerization, ie the union of many molecules into macromolecules, plays an important part in biological syntheses; nucleic acids, starch and celluloses are formed in this way.

(4) Organic deposits, such as coal and oil, are evidence of the photosynthetic activity of plants in the geological past.

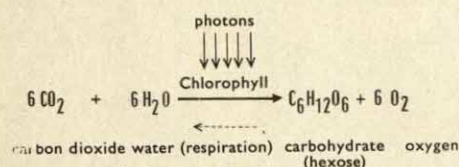


Fig. 1. Diagram representing chlorophyll respiration.

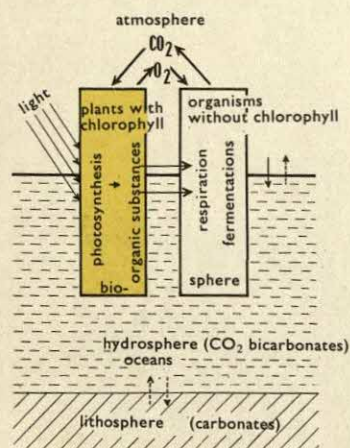


Fig. 2. The carbon cycle of terrestrial and marine organisms.

Neither knowledge of its structure, nor demonstration of the products it makes, is sufficient to explain how the organism acts as a chemical factory. Energy exchange is the most important characteristic of life. Every living thing is plunged into a tide of transformations, of building-up and breaking-down, of organic syntheses and of movements of basic mineral materials that link the future with the past. All the chemical elements that make up living matter must pass through such a cycle. Both the life of each individual, and the continued existence of all the living things on earth (ie the 'biosphere') depend on the co-ordinated action of the different mechanisms of this cycle.

The carbon cycle has a special importance. Two types of organism are involved, those with chlorophyll and those without (which may be either plants or animals). It is the green plants that catch the sun's rays by means of their pigments, and thereby harness the whole life-cycle to this extra-terrestrial 'power-station', which in turn obtains its energy from atomic changes within itself. This mode of use of atomic energy has been an attribute of plants for hundreds of millions of years. Although man may think himself master of the living world, he is completely dependent on it. His own efforts to harness the sun's energy are quite insignificant beside the achievement of plants.¹

The chemical reaction whereby plants convert light energy into chemical energy, which is retained in the form of organic compounds, is called photosynthesis.²

Photosynthesis also involves gas exchanges; carbon dioxide is taken from the air and oxygen returned to it. The 'photosynthetic quotient', O_2/CO_2 , is 1, for the volumes of the gases are equal, when the reaction follows the diagram in fig. 1. The resulting organic product (carbohydrate, hexose or sugar) may form the basis for other syntheses within the cell. It is often merely polymerized into starch, and deposited in the form of this insoluble compound of high molecular weight.³ The demonstration of gaseous exchanges or the

formation of starch has long provided evidence of photosynthesis; but as we shall see later much more sensitive methods are now available, such as those using radio-active carbon.

In the carbon cycle, respiration has an opposite effect to photosynthesis (fig. 2). The former process involves the consumption of oxygen and the production of carbon dioxide, and it is associated with the breakdown of organic substances, usually carbohydrates. Furthermore, whereas photosynthesis converts light energy into chemical energy which is stored in the form of sugars, respiration liberates energy from these and makes it available for all the mechanisms needed to maintain the life of the organism. Of course, only a small part of the carbohydrate formed by photosynthesis is used up by respiration to provide energy. The greater part provides the raw material with which protoplasm carries out its chemical syntheses.

The following details of the varying amounts of carbon dioxide in nature supplement fig. 2 and give an idea of the quantities of matter involved.

In the earth's crust (lithosphere) there are about 25 thousand billion (25×10^{15}) tons of carbon, mainly in the form of calcium carbonate or limestone (organic remains such as coal and oil form only 0.03 per cent of this total⁴). The waters of the earth (the hydrosphere, fundamentally, the oceans) contain 36 billion

(36×10^{12}) tons of carbon, principally in the form of bicarbonates. The atmosphere contains only 700 thousand million tons of carbon (0.7×10^{15} kg., ie 2.6×10^{15} kg. of CO_2). The proportion of carbon dioxide in the air at ground level is 0.03 per cent by volume. Finally, all living creatures (the biosphere) contain at the present time about 130 thousand million tons of carbon (1.3×10^{14} kg.).

The green plants of the earth withdraw about 40 thousand million tons (4×10^{13} kg.) of carbon dioxide per year from the air; 60 per cent of this is fixed by forests (which occupy 30 per cent of land not covered by ice), 32 per cent by cultivated plants (occupying 26 per cent of dry land), and the rest by the weeds of steppes and deserts and the plants in large cities. It is calculated that as much CO_2 as exists in the whole of the atmosphere passes through the biosphere once in about every 60 years. The oxygen cycle is about 700 times as long, because of the greater concentration of this gas in the air (20.8 per cent).⁵

Under present conditions, the production of CO_2 and the corresponding consumption of O_2 by the respiration of the 'non-green' beings of the earth balances the use of CO_2 and the emission of O_2 by photosynthesis. The geochemical production of CO_2 ('new' CO_2 liberated by volcanic eruptions) is small in amount. Much the greatest quantity (about 90 per cent) of CO_2 is produced by the plants and animals of the soil (bacteria, fungi and small animals); big animals (9 per cent) and even the whole of humanity (less than 1 per cent) play only a small part in this.

During the last century, however, it is man who has brought about the greatest changes in carbon compounds. It has recently been estimated that the production of CO_2 by industry, engineering and transport, at the expense of the organic reserves laid down during past epochs of geological time, will soon reach a quantity equal to one-sixth of that introduced into the carbon cycle by the whole of the biosphere. Nevertheless, it is possible to detect only a slight increase in carbon dioxide in the air, so it must be assumed that the excess of CO_2 produced dissolves in the hydrosphere. The carbon reserves laid down in past geological periods are bound to disappear in time, and this process is being accelerated by the steadily increasing manufacture of artificial synthetic products.

The carbon cycle of the hydrosphere works in the same way, but probably more rapidly than that of dry land. Here the photosynthetic producers are the algae which

colonize the rocks of our coasts in dense groups to a depth of about 20 metres, and above all the countless microscopic floating plants that make up an important part of the plankton of the upper strata of the seas. Here also there is a dynamic equilibrium between the fixers and the users of carbon, the latter being plants without chlorophyll and animals of every size living at all depths of the oceans.

The problem of the carbon cycle in nature is a complicated one, and the figures given above are not universally accepted. However, the results of the International Geophysical Year have added considerably to our knowledge of this subject (see K. Buch, 1960; D. Müller, 1960).

Autotrophy and heterotrophy

We call 'autotrophic' those organisms with chlorophyll that can make their own carbon compounds by photosynthesis, and the non-green organisms that require a supply of carbon in organic form are called 'heterotrophic'. Autotrophic organisms, capable of utilizing mineral elements in their organic syntheses, provide essential nourishment for heterotrophic organisms.

In the study of the physiology of nutrition, admittedly, the terms 'autotrophy' and 'heterotrophy' are used in a wider sense, to indicate the power to transform various elements from the mineral to the organic state, or the lack of that power. In the present case, however, we are speaking only of autotrophy (or heterotrophy) for carbon. Similarly there are autotrophic or heterotrophic organisms with respect to other cycles; for example, some are autotrophic as regards nitrogen and can use nitrates, ammonium salts, or even nitrogen gas, while those that are heterotrophic need to be supplied with organic nitrogen in the form of amino-acids or proteins. Autotrophy for nitrogen is commoner in nature than that for carbon.

Carbon autotrophy depends, in nearly all cases, on the utilization of light energy (photosynthesis). Certain groups of bacteria, however, can replace light, as a source of energy, by the oxidation of substantial quantities of organic matter.⁶ The energy produced by this oxidation serves to reduce the CO_2 to carbohydrates: this is chemosynthesis. Although these microbes play only a small part in the carbon cycle as a whole, they are of great interest to physiology, and also because of their participation in other cycles. The most important of these is the oxidation of ammonia

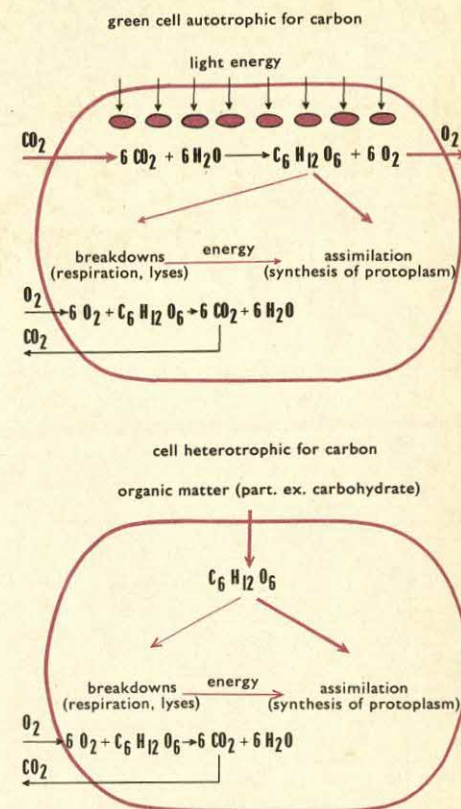


Fig. 3. The metabolism of an autotrophic green cell. Above: photosynthesis provides the cell with carbohydrates. Below: respiration uses part of these carbohydrates; another part goes to build up protoplasm.

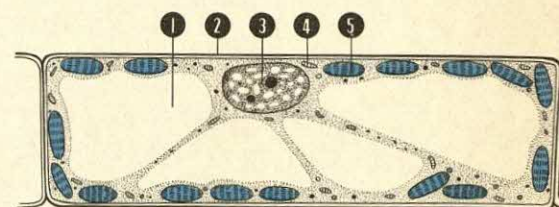


Fig. 4. Diagrammatic representation of a photo-autotrophic cell: (1) chloroplast; (2) mitochondrion; (3) nucleus; (4) cellulose membrane; (5) vacuole (viscous liquid).



Fig. 5. Photograph, taken by electron microscope, of a thin cross-section through a chloroplast of the aquatic plant *Elodea canadensis*. (Photo Mühlethaler and Frey-Wyssling, Zurich).

(5) Photosynthesis is certainly the most important chemical reaction in the world, by reason of the great mass of substances it transforms.

(6) In contrast with the photosynthesis of chlorophyll-containing organisms, the chemosynthesis of certain bacteria achieves a different method of autotrophy by using the energy of chemical reactions.

(7) The cell is a little factory, whose machine-tools are differentiated structures, each specializing in the performance of one particular function.

(8) Plants have successfully gambled by exposing an enormous surface for gaseous exchange, while avoiding the loss of too much of the water that is so essential for life.

to nitrates by the nitrifying bacteria: this oxidation serves as a source of energy to them for the reduction of CO_2 , and such bacteria are called chemo-autotrophic. This chapter, however, will deal only with the green plants with chlorophyll that produce organic substances by photo-autotrophy. Let us now examine the chemical transformations effected by organisms both autotrophic and heterotrophic for carbon, at cellular level.

Synthetic powers of the cell

The exchanges of substances carried out by a cell are represented in fig. 3. The green cell owes its photosynthetic ability, which is its fundamental characteristic, to the possession of minute internal organs containing chlorophyll: the chloroplasts. All the processes of metabolism, other than photosynthesis, are basically the same in both autotrophic and heterotrophic cells. Both types of cell use carbohydrates in their metabolism (respiration or breakdown) and in their syntheses (assimilation). The green cell also breathes, as can easily be demonstrated by placing it in darkness. Its respiration is then unmasked, as photosynthesis is in abeyance. On the other hand, it is difficult to determine whether the respiration of green cells is the same in the light as in darkness. One cannot, in fact, easily observe respiration during photosynthesis because the two processes are contrary, and respiration accounts for only a small fraction ($1/10$ to $1/50$) of the total gaseous exchange.

The similarity between autotrophic and heterotrophic cells in protoplasmic assimilation, shown in fig. 3, should be accepted with reservation in the present state of knowledge. There is, in fact, some evidence that the synthesis of the proteins and nucleic acids of protoplasm can also be directly stimulated by the photosynthetic process. Photosynthesis would then be not only a method of manufacture of carbohydrates, but could perhaps be involved also in the production of other constituents of the cell. In this event, photosynthesis would no longer follow only the above equation; but further studies are necessary to show whether such a process does actually occur. Anyhow, we can accept the data given in fig. 3 as a first approximation.

In photosynthesis, as in respiration, the cycles of hydrogen and oxygen are closely connected with that of carbon. In the process of assimilation, they take part in the metabolism of other essential elements, and thus their cycles link with those of nitrogen and sulphur in the synthesis of proteins. When the

cell disintegrates, all these elements return to the mineral state.

The chloroplasts of green cells

It has been established that there is a division of labour in the cell and that each physiological function is carried out by one particular component.⁷ Photosynthesis takes place in the chloroplasts, respiration in the mitochondria, and protein synthesis—at least in part—is controlled by the nucleus, which also contains the vehicles of heredity. Other specialized structures (eg the ribosomes, spherosomes, and the reticulum) undoubtedly have functions of assimilation. Fig. 4 is a simplified diagram of a cell showing chloroplasts, the organs of photosynthesis. Mitochondria, the organs of respiration, usually appear only in small numbers in green cells.

Although we are dealing here with chloroplasts only, the general organization of a green plant must not be forgotten. Photosynthesis requires definite relationships between light, air and the plant. The structure of a plant is characterized by its extensive surface, which provides suitable conditions for the absorption of light and the free exchange of gases. It is the leaves that are the most distinctive feature of a plant. The so-called 'open' pattern of a plant, whose shoots, leaves and roots grow apart, contrasts with the 'closed' organization of an animal. The latter, for its part, has developed a bigger internal surface for its nutrition and the gaseous exchanges of its tissues. The extent of their outer surface condemns plants to life in one place, and also presents a difficulty of water supply, which is inevitably aggravated by considerable transpiration at the leaf-surfaces. But plants have successfully adapted themselves in a number of ways to meet the often conflicting requirements of photosynthesis and the conservation of water.⁸ Let us now enlarge a little on this interesting example of biological adaptation. A plant could not reconcile the advantages and disadvantages of its extensive surface if its cells were not strengthened by elastic cellulose walls. The large internal vacuoles give the living cells, well supplied with water, a blown-up balloon's resistance (turgescence). Groups of dead cells with thick walls, having considerable mechanical strength, further reinforce the plant's solidity. Even more remarkable than the surface formed by the leaves is that developed by the chloroplasts themselves within the cells. It has been estimated that in a 110-year-old beech tree, 25 metres high and covering an area of 150 square

metres, the leaves have an area of 1,200 square metres and the chloroplasts expose a surface of 18,000 square metres (fig. 7). Similar relationships are found in aquatic plants, whose extensive surface facilitates not only the absorption of light, but also that of dissolved CO_2 or bicarbonates. But chloroplasts do not always achieve this increase in their effective surface in the same way. Certain green algae have developed characteristic chloroplasts of complicated shapes (fig. 9). It seems that with the development of species provided with stems, the most advantageous way the chloroplast-substance can be distributed in the cells is in the form of numerous lens-shaped bodies. We find this arrangement already in some algae, in most mosses, and in all higher plants.

The electron microscope has demonstrated convincingly that this development of the surface of the chloroplast is continued in its understructure. Fig. 5 is a photograph taken by electron microscope of a very thin section across a chloroplast of a higher plant. It shows a number of double layers compressed at many points so as to form thick bundles. These bunches are called 'grana', and the less thick areas are the 'stroma'. The grana contain nearly all the chlorophyll. It is possible that the chlorophyll molecules are arranged in layers of single thickness, but at present there is considerable dispute about the origin of this structure. The chloroplasts are formed from undifferentiated rudiments, and the double layers seem to arise from vesicles which subsequently become flattened. The chloroplasts of algae often have a simpler structure, the layers being more homogeneous throughout their surface. However, it is very doubtful whether their lack of grana is altogether typical.

The chloroplasts of green algae and of higher plants contain quite a variety of pigments: first, two types of chlorophyll (there is about 3 times as much chlorophyll *a* as chlorophyll *b*), then the carotinoids, essentially β -carotin and its products of oxidation, the xanthophylls. The primary pigment of photosynthesis is, according to the majority of research workers, chlorophyll *a*.⁹ Some interesting theories have been advanced about the part played by carotinoids in the process of photosynthesis, but no definite conclusion has yet been reached. As the formula in fig. 6 shows, in its molecular structure chlorophyll resembles haem, the coloured portion of the blood pigment haemoglobin, but the functions of the two pigments are entirely different. It is important to note the presence in the chloro-

plasts (although in smaller quantities than chlorophyll) of cytochromes, which belong to the group of haems and which are also found in mitochondria. The particular structure of the chlorophyll molecule causes it to be

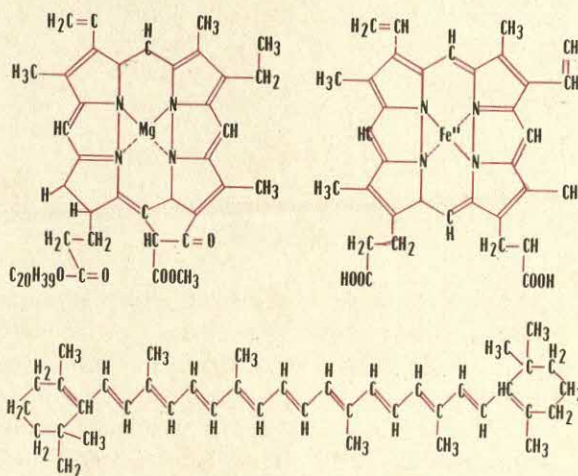


Fig. 6. This diagram represents the molecular structure of chlorophyll.

arranged in a way determined by the anatomy of the chloroplast, which in turn is adapted to hold the pigment. This arrangement is a basic requirement for the function of photosynthesis. Several groups of autotrophic micro-organisms also show remarkable peculiarities in their fine structure and in their variety of pigments.

Red algae have softer and more pliable chloroplasts than those of green plants. Their structure is typically lamellar, but their pigments show two differences. Chlorophyll *a*, essential for the conversion of light into chemical energy, is always present; but chlorophyll *b* is absent. They also contain phycoerythrin, a red pigment, protein in nature, whose colour predominates; and traces of a chemically related blue pigment, phycocyanin.¹⁰

Blue algae have no individual chloroplasts, but lamellae of chlorophyll scattered throughout the protoplasm. The structure of these lamellae is very similar to that of the true chloroplasts. Besides chlorophyll *a*, they have phycocyanin and small quantities of phycoerythrin. The presence of considerable amounts of phycoerythrin in red algae, and of phycocyanin in blue algae, extends for these plants the possibility of utilizing the green or orange light absorbed respectively by these two pigments (fig. 8).

Certain green and purple bacteria can use light as a source of energy and thus assimilate carbon dioxide. It is necessary for them to have available also a reducing substance:

(9) Chlorophyll *a* ensures the conversion of light into chemical energy, and the other photosynthetic pigments serve only to transfer to it the photons they absorb. They are adjuvants, which increase the capacity of plants to absorb light.

(10) Phycoerythrin and phycocyanin are red and blue pigments respectively, found in algae of those colours. They are heteroproteins consisting of ordinary proteins and 'chromogens' whose structure is similar to that of bile pigments.

(11) The chlorellae are microscopic green freshwater algae. They are in the form of tiny spheres only a few microns in diameter, very active in photosynthesis.

(12) A hydrogen carrier, such as triphosphopyridine nucleotide, effects the transfer of hydrogen from water to fixed carbon dioxide. This substance is related to the nucleotide constituents of the nucleoproteins of cell nuclei and cytoplasm.

(13) Conveyors of energy are also involved. One of the most important, adenosine-triphosphoric acid, plays a similar part in energizing the contractions of our muscles.

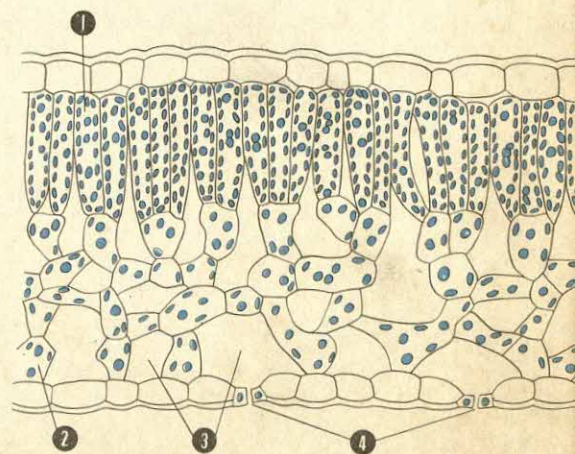


Fig. 7. Cross-section of a green leaf. Above, the parenchyma, i.e. palisade tissue (1) with many chloroplasts; below, spongy chlorophyll tissue (3) consisting of cells (2) with many spaces between. At the under surface there are stomata (4) through which gases enter and leave.



Fig. 8. Blue algae.

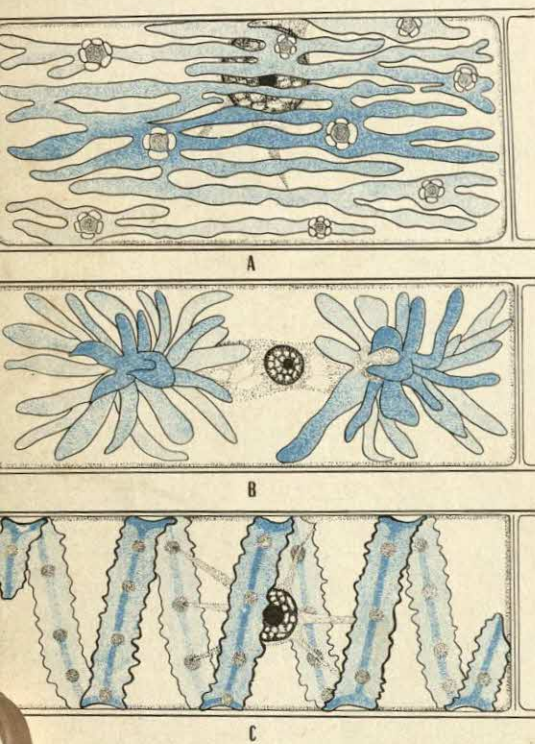


Fig. 9. Cells of algae showing different kinds of chloroplast: (a) reticular chloroplast of *Oedogonium*; (b) star-shaped chloroplast of *Zygnema*; (c) spiral chloroplast of *Spirogyra*.
(14) The survival of some photosynthesizing bacteria from the distant past may be evidence of the long process of evolution that has resulted in the elaborate mechanism of chloroplasts.
(15) The process of reduction involves the loss of oxygen or the uptake of hydrogen by molecules, and requires energy. Oxidation involves the opposite process and liberates energy.

sulphur, a sulphide, or some organic substance. Their photosynthetic organs consist of globules rich in proteins and fats and also containing particular kinds of chlorophyll, bacteriochlorophylls. The minute structure of the globules shows lamellae similar to those of chloroplasts. Some of these photo-reducing bacteria are so rich in carotinoid pigments that they are red in colour.

The photochemistry of photosynthesis

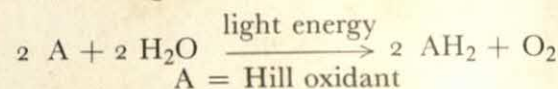
The chemical reactions that take place in chloroplasts are one of the most debated problems of present-day biology. We must mention that the equations given above show only the beginning and end-products of a very complicated series of operations. This series may be divided into two entirely different types of reaction:

(1) A photochemical reaction that may be likened to the effect of light on a photographic plate. Its speed depends on the intensity of light, but not on temperature.

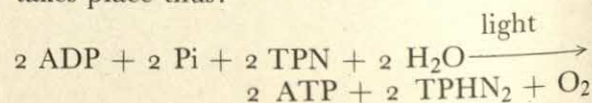
(2) A series of 'dark' or non-photochemical reactions that may be roughly compared to the development of photographic plate in the dark. Their speed is independent of light, but varies with the temperature.

Our knowledge of these matters is due particularly to the work of Willstater and Stoll (1918) and of O. Warburg. Following the work of Warburg, the use of a very suitable organism, the unicellular alga *Chlorella* (fig. 11), has played a decisive part.¹¹ The various dark reactions have been found to consist of numerous stages, which, like all the processes of both plant and animal metabolism that are independent of light, are governed by enzymes. The study of these reactions was at first attended by great difficulties because the biochemists, although they had suitable methods

available, could not separate the photosynthetic reactions from the living cell and study them *in vitro*, independently of the other reactions of plant metabolism. It was not until 1937 that R. Hill succeeded in isolating from leaves some chloroplasts that still retained at least part of their photosynthetic apparatus almost intact. These preparations could no longer fix CO₂, but on exposure to light they produced oxygen provided they were supplied with reducible substances in place of CO₂. Of these substances, or 'Hill oxidants', the first discovered was potassium ferricyanide. In general, 'Hill reactions' proceed according to the following scheme:



This biochemical fraction of photosynthesis shows that the reduction of CO₂ and the liberation of O₂ are two separate parts of the complete mechanism of photosynthesis. The origin of the oxygen from water, and not from CO₂, was then confirmed by Ruben and his colleagues (1941) using the heavy isotope of oxygen with an atomic weight of 18. In this way they were able to confirm the hypothesis of Van Niel (1931) that the splitting of water would prove to be fundamental to photosynthesis.¹² The later reduction of CO₂ by hydrogen originating from the water, and the liberation of oxygen, are part of the dark reactions (fig. 12). This hypothesis has long been of great value in research on photosynthesis, but now it no longer seems able to account for all the observations; and so Arnon (1960), also on the basis of experiments with isolated chloroplasts, has put forward another hypothesis. This depends on the fact that by progressively increasing the factors favourable to photosynthetic activity, it is possible to demonstrate different reactions to light: (1) Hill's reaction proper; (2) 'photosynthetic phosphorylation' with or without liberation of oxygen: this is to do with the entry of phosphoric acid into combinations rich in energy, such as adenosine triphosphoric acid (ATP); and (3) complete photosynthesis. Photosynthetic phosphorylation with liberation of oxygen is of special interest in the analysis of photosynthesis, and in biochemical terms it takes place thus:



where ADP denotes adenosine-diphosphoric

acid; Pi, phosphoric acid or 'inorganic' phosphate; and TPN, triphosphopyridine nucleotide, which acts as a carrier of hydrogen, combining with it to give the reduced form TPNH_2 .

In the process of photosynthesis, the sequence of reactions is indicated in fig. 13. Under the influence of light, chlorophyll gives off electrons which, with hydrogen ions H^+ arising from the dissociation of water and with TPN, go to form reduced TPNH_2 . The hydroxyl ions OH^- of the water give their electrons to the cytochromes of the chloroplasts and oxygen is evolved. Finally, the cytochromes return to the chlorophyll its lost electrons. In the course of these reactions, ATP, which is rich in energy, is formed from ADP and mineral phosphate.¹³ Then the reduction of CO_2 occurs by hydrogen carried by the TPNH_2 , with the aid of energy provided by ATP, according to reactions to be described in subsequent paragraphs. This hypothesis differs from that of Van Niel in that the separation of water into its two constituents is not effected directly by light, but through the intermediate action of TPN and cytochromes, enzymatic systems that are well known in 'dark' metabolism. This new theory links the phosphorus and carbon cycles closely together.

Since photosynthesis requires the presence of organic compounds as complicated as those of the chloroplasts, it is obvious that photoautotrophy, the central process around which the whole of present-day life on earth revolves, cannot have existed since the beginning of the living world.¹⁴ Many investigators think that life began by the progressive development of carbon and hydrogen compounds of mineral origin. The first living things would then have led a kind of heterotrophic existence in surroundings still devoid of oxygen. Light energy could be of use to life only after the development of chlorophyll, and then the biosphere took a great step forward. In this process, according to Arnon, the phenomena of phosphorylation played a special part as preparatory stages for photosynthesis. The reduction of CO_2 , the splitting of water, and the liberation of oxygen would no doubt be later chapters in the story of living protoplasm, but they must certainly have been written long before life developed the variety it has today. These hypotheses are admittedly speculative, but they are not without foundation. There are in fact, among micro-organisms, certain primitive forms such as photosynthetic bacteria and certain flagella that even today seem to show primitive stages of photosynthesis.

Metabolism of carbon in the absence of light

As previously explained, chlorophyll-bearing plants assimilate carbon dioxide, water, and various mineral salts. From the standpoint of the chemistry of carbon, photosynthesis consists of a reduction of carbon dioxide by the hydrogen of water, whose oxygen is liberated.¹⁵ It may be represented by the chemical equation given in fig. 1. The formation of a gram-molecule of glucose corresponds to the storage of 696 'large' calories.

The substances most quickly elaborated by plants are sugars and starch. Their formation is achieved by many intermediate reactions, which little by little improve the nutritive molecules. The syntheses, which take place at ordinary temperatures, proceed in several successive stages. Knowledge of these stages was hampered until some fifteen years ago by

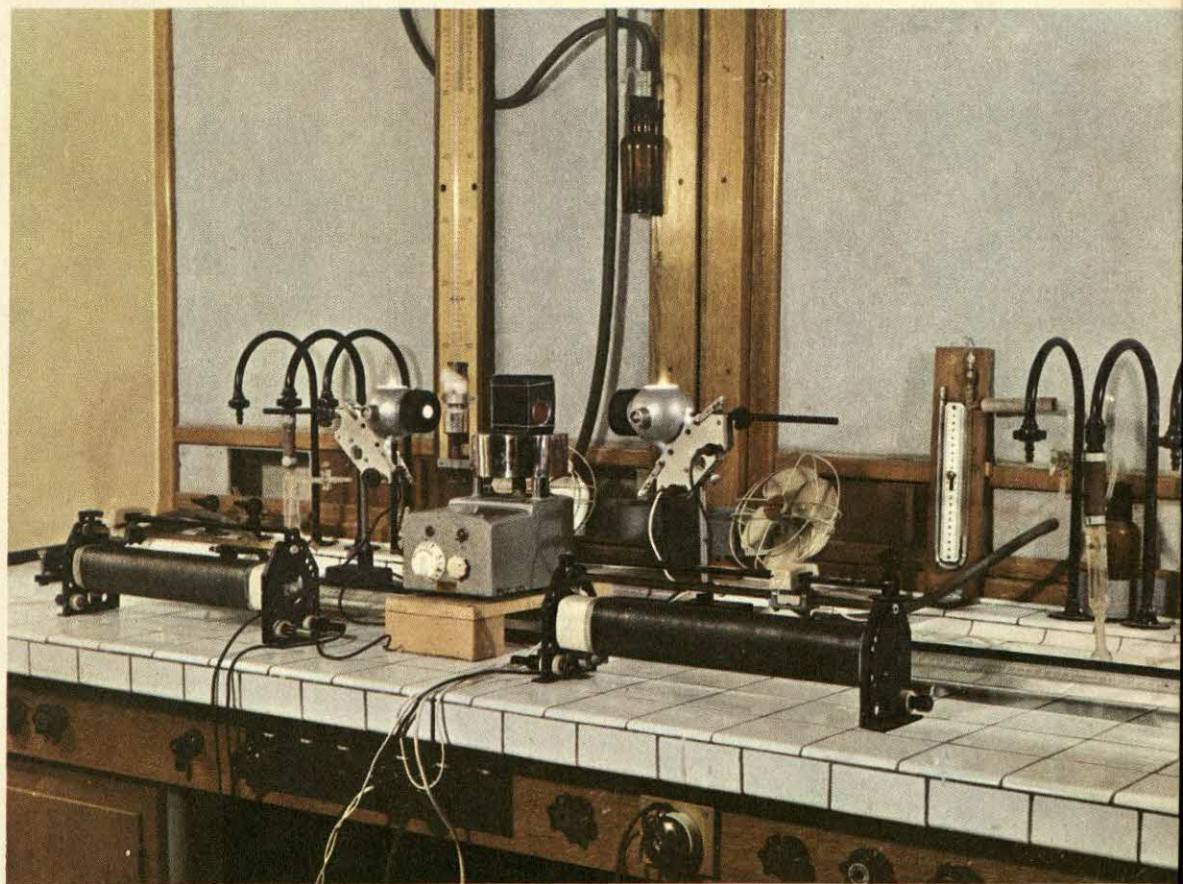
(16) Radio-active carbon, with an atomic weight of 14, differs from ordinary carbon (^{12}C) not only in atomic weight, but also in that it emits β -rays (electrons). It is obtained by the bombardment of nitrogen with neutrons.

(17) The reduction of an organic acid, phosphoglyceric acid, replaces that of carbon dioxide. This acid is itself formed in the process of fixation of carbon dioxide.

(18) Cyclical reactions, whose early stages result in the reformation of active molecules, are a common type of biological mechanism.

(19) Carbon dioxide and hydrogen 'enter' the cycle, and the accumulated products 'leave' it.

Fig. 10. Apparatus for the study of photosynthesis: algae are enclosed in the small black box with windows covered by red filters. Light is provided by arc-lamps on either side; radio-active carbonate is introduced into the box at the moment illumination begins. After a short period, the algae are dropped into boiling alcohol in order to arrest all the photosynthetic reactions. (Photo: Laboratory of Photosynthesis, C.N.R.S.).



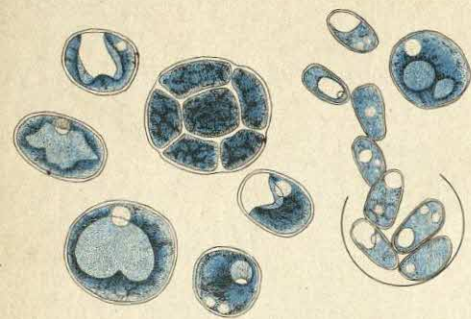


Fig. 11. *Chlorella pyrenoidosa*, the subject of much research in photosynthesis and plant physiology since the pioneer work of Warburg. (After Warburg).

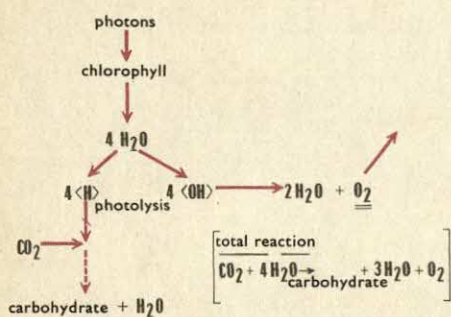


Fig. 12. Hypothesis of the photolysis of water according to Van Niel (1931).

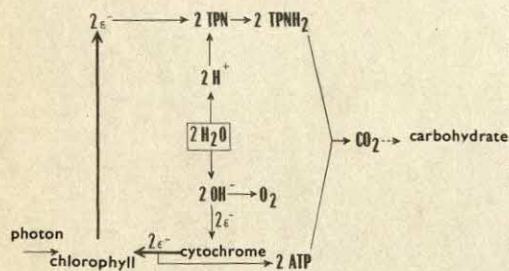


Fig. 13. Arnon's hypothesis (1960) of photosynthetic phosphorylation. Electrons (e^-) split off from chlorophyll and furnished with additional energy through the action of photons, come back to the chlorophyll after having effected the decomposition of water and the formation of adenosine triphosphate.

several difficulties. Firstly, the stages are rapid, and difficult to discern. Then, the intermediate substances are formed in small quantities, and are usually unstable. Finally, how can one distinguish a molecule of glucose, newly formed as the result of a flash of light, from a molecule previously present in the cell, whose origin might be quite different? There was no lack of theories when in 1939 the American chemist, S. Ruben, of the University of California at Berkeley, applied a new method of investigation: the use of radio-active carbon, an isotope of ordinary carbon.

When a plant takes up carbon dioxide whose carbon is radio-active, this carbon enables one to distinguish the newly-formed molecules from those of the same chemical nature that were already present, because the former will be marked by radio-activity.

Ruben used a tiny freshwater alga of the genus *Chlorella*, suspended in water. He rapidly added several drops of a solution of bicarbonate marked by radio-active carbon of atomic weight 11 and, after a few minutes' illumination, he sought for radio-active substances. He did not succeed in isolating the intermediate stages, because ^{11}C loses its radio-activity very rapidly (it loses one half only 20 minutes after its origin, from the bombardment of boron atoms with protons). But the way was now clear. A few years later, his successor, M. Calvin, used another isotope, ^{14}C , whose half-life is 5,000 years, and repeated Ruben's experiments¹⁶ (fig. 10).

Calvin also used a method of analysis discovered during the second world war, namely paper chromatography. This permits the rapid separation of soluble substances in a mixture, based on their different speeds of movement up a piece of blotting paper suspended vertically and washed in a mixture of suitable solvents.

The results obtained by the exhaustive work of a large team of research workers are one of the most important chapters in plant physiology.

Carbon dioxide is fixed in the chloroplasts of the cells, alike in light or darkness, on the molecules of a carbohydrate with 5 carbon atoms, ribulose diphosphate, which breaks up. There result two molecules of an organic acid: phosphoglyceric acid.¹⁷ Thus an old hypothesis of Liebig's, postulating organic acids as intermediaries in photosynthesis, was unexpectedly confirmed. The existence of this reaction was proved by the almost exclusive localization of the radio-carbon in phosphoglyceric acid, when the plants were in contact with

marked carbon dioxide only for a few seconds. Next, reduction by the hydrogen of water attacks the carboxyl group of the acid, which is converted into a triose, or carbohydrate with 3 carbon atoms: phosphoglyceric aldehyde, capable of being isomerized into another triose, dihydroxyacetone phosphate (fig. 14). The reduction of phosphoglyceric acid is the main chemical reaction that enriches the carbon chains with hydrogen and with energy.

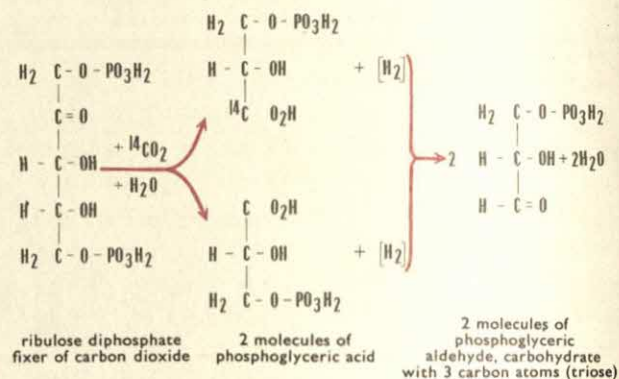


Fig. 14. The fixation and reduction of carbon dioxide. At first, only one carboxyl group (the acid radical— CO_2H) of one of the two phosphoglyceric acid molecules is radio-active.

The later reactions are all of the nature of condensations, for which trioses are the raw materials. They begin by the formation of fructose diphosphate from two molecules of triose phosphate, and the fructose in turn is the basis of a series of reactions ending in the formation of a saccharose or starch.

Their outstanding characteristic is that a part of the molecules of fructose and one of triose phosphate combine together to reconstitute the original fixer of carbon dioxide, so that this agent is constantly being replenished in the course of a cycle of reactions.¹⁸ At each stage of the cycle a molecule of carbon dioxide is taken up and integrated into the carbon chain of a carbohydrate (fig. 16). Carbohydrate molecules gradually leave the cycle and accumulate in the cells.¹⁹ With the aid of hydrogen, whose utilization it makes possible, light energizes the cycle by the continual formation of trioses from phosphoglyceric acid.

The reactions are very rapid, and the trioses are radio-active a few seconds after 'tagged' carbon dioxide has been added. Saccharose and starch are marked in less than a minute. Similar results have been obtained with all the plants experimented upon up to

now, but certain slight differences have been found. For example, polymers of fructose are formed in the leaves of Gramineae, but starch is formed in most other leaves (fig. 15).

In some unicellular algae, fatty substances are deposited; while in the chlorellae there is a rapid accumulation of proteins as well as starch.

All these reactions are accelerated by diastases or enzymes, of which the majority are now known. Nearly all are reversible reactions, ie they can proceed in either direction. The energy and reducing power acquired from the assimilation of photons absorbed by chlorophyll pigments determine the direction in which these reactions proceed. Although every gram-molecule of glucose or fructose formed corresponds to the fixing of 696 large calories, the energy supplied in the form of photons must be much more than this, for the maximum production of light energy by photosynthesis is not more than 30 per cent. This is a figure obtained under optimal conditions in the laboratory, but in natural conditions the efficiency with which sunlight is converted into chemical energy found in synthesized plant substances is at most 1 per cent.²⁰

Fermentation and respiration

Plants breathe during the day just as they do at night, and the material used is generally carbohydrate. A leaf provided with starch by its photosynthesis, a stem or a root obtaining soluble sugars in the sap originating from the leaves, a fungus finding its food in the form of organic molecules in the humus of the earth, a germinating grain of wheat, all use glucose in the end as a source of energy.

Each gram-molecule of glucose yields back 696 large calories upon complete oxidation, the reverse of photosynthesis. But whereas direct combustion would liberate these calories all at once in the form of heat, inducing an appreciable rise of temperature, the respiratory processes are much more gradual and more flexible. Like photosynthesis, the breakdown takes place in a series of stages, each differing from the preceding one only in a slight alteration concerning but some of the atoms of each molecule.

Several glucose-attacking mechanisms are known; and studies made with them, using organic molecules marked with radio-active carbon atoms, have enabled the course of the breakdown to be better followed.

However, the first known among the mechanisms was alcoholic fermentation, whose main features were established about thirty

years ago, long before the use of marked molecules.

Pasteur had already described the action of yeast in the brewing of beer, its occurrence in the absence of oxygen, the importance of phosphates in the process, and its energizing characteristics. It was also known that potatoes and fruits could be fermented anaerobically. Recent work has demonstrated the great reactivity of combinations of carbohydrate and phosphoric acid molecules. The formation of phosphoric compounds always begins the process, which results in the same triose-phosphates whose place in the photosynthetic cycle we have seen. The key-reaction is the oxidation of one of them, phosphoglyceric aldehyde, into phosphoglyceric acid, the reverse of the reaction already described. Simplification of the molecules then occurs by the loss of hydrogen and carbon dioxide. In the absence of air, the hydrogen split off reduces the residual carbon chains to alcohol. The reactions preceding this last stage are only the reverse of those essential to photosynthesis. Everything happens as if plants could equally well carry out synthesis or breakdown of organic molecules, by a series of practically reversible reactions. The direction of the reactions is controlled by the balance of energy, which is positive for chlorophyll-containing cells in the light, but negative for them in the dark and for the other cells all the time.

In the presence of oxygen, oxidation is more complete than under anaerobic conditions, and although the intermediate stages are the same, at least up to phosphoglyceric acid, the final reactions are much more complicated. A true cycle develops again. It takes place at the level of the mitochondria, cellular organs even smaller than the chloroplasts (fig. 18). Several organic acids are involved. The detachment of hydrogen from their molecules and the splitting-off of carbon dioxide take place in turn (fig. 17). The hydrogen is held temporarily by transporters, as in photosynthesis, and is finally oxidized by oxygen from air, not in an explosive manner, as when a mixture of suitable proportions of the two

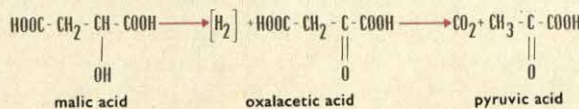


Fig. 17. Two stages in the oxidation of malic acid, with loss of hydrogen and carbon dioxide.



Fig. 15. Young chloroplast in a leaf-cell of *Elodea canadensis*, showing the lamellae not yet separated into grana. Under the influence of light, it has synthesized starch which is deposited within the chloroplast. (Photo: Professor R. Beuvet, Botanical Laboratory, École Normale Supérieure, Paris).

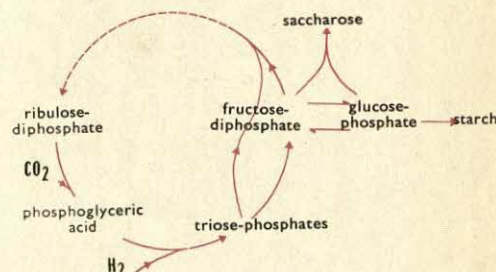


Fig. 16. Simplified cycle of the metabolism of carbon in photosynthesis.

(20) Under natural conditions the amount of energy produced by photosynthesis is small compared with the enormous quantity of organic matter formed. This is about 50 to 80 thousand million tons per year on land and sea. (21) Vitamin B₆ acts as a catalyst for the process of transamination, ie the interchange of the amino-group (>CH-HN₂) of an amino-acid with the ketone groups (>C=O) of a ketonic acid. Only nitrogen, hydrogen and oxygen atoms are exchanged, those of carbon remaining in their original molecules.

(22) *The metabolic cycle of development and reproduction of plants, from the germination of the seed to the maturation of new seeds, is superimposed on the cyclical mechanisms of photosynthesis and respiration.*



Fig. 18. Photograph, taken by electron microscope, of a cross-section of a leaf of *Elodea canadensis*, showing bodies with many ridges side by side with a chloroplast in which grana can be seen. These bodies are the mitochondria, where respiration takes place. (Photo, mag. 50,000: Professor R. Beuvat, Botanical Laboratory, École Normale Supérieure, Paris).

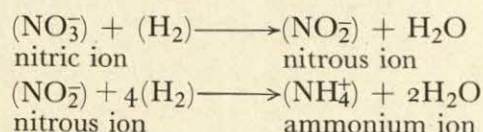
gases is ignited, but in the course of reactions involving transporters and enzymes in an aqueous medium.

The energy liberated by oxidative reactions is not always lost. When a reaction generates enough energy to provide for a pyrophosphate linkage, adenosine-triphosphoric acid is formed and the energy retained therein can be utilized later for syntheses.

As a final masterpiece of versatile complexity, different intermediate products of oxidation can give rise to the materials necessary for the synthesis of amino-acids, constituents of the proteins of protoplasm. Thus the building-up of protoplasm depends on breakdowns which provide both energy and carbon molecules suitably re-arranged. The formation of glutamic acid, one of the commonest amino-acids, depends on the respiratory cycle of organic acids. The formation of fats from the carbon chains of sugars is caused by the same grafting of synthesis on to breakdown of molecules. In this case also, the reverse reactions convert fats back into sugars, as in the germination of oily seeds.

Whereas photosynthesis and the intermediate stages of oxidation provide both the energy and the carbon chains necessary for the synthesis of the amino-acids that constitute proteins, the nitrogen of plant amino-acids usually comes from nitrates in the soil.

The dead bodies and waste materials of organisms decomposed by bacteria yield simple molecules. Urea and ammonium salts are converted by other bacteria in the soil into nitrates. Plants, having absorbed the nitrates, reduce them to nitrites, then to ammonium salts whose ammonia will re-enter organic molecules. The series of reactions involving the reduction of nitrates, is represented thus:



It is constantly taking place in both the roots and the leaves of plants.

The necessary hydrogen is brought by the same transporters that are concerned in the syntheses and breakdowns of carbon chains; only the catalytic enzymes are different. The transfer of ammonia to carbon chains is brought about through the agency of vitamin B₆ or pyridoxin, found in abundance in germinating seeds, where there is intense production of protein.²¹ This vitamin can also effect the transfer, by the process, of transamination, of the amino-groups of various

amino-acids to the corresponding ketonic acids.

The condensation of amino-acids into proteins, whose molecules are very large and very varied (their molecular weights rising from under 100,000 to several million) takes place in at least two stages. The first consists of the arrangement of the amino-acids in their proper places in relation to each other, like the pieces of a jigsaw puzzle. The second is the linkage of the amino-acid molecules.

In contrast with the molecules of carbohydrates built up in the first place by photosynthesis, the formation of protein molecules requires the participation of partial breakdown reactions, of aminations, and of resynthesis, which more or less profoundly modify the carbon chains originally deposited in the cells.

The building-up of the substances constituting a plant involves many reactions. Their occurrence is determined by the available energy, whose primary origin is the sun's rays.

While syntheses take place by the reduction of carbon dioxide, breakdowns consist essentially of oxidations which restore this substance to the carbon cycle of the mineral world. But the paths by which these reactions proceed are not always straight. A substance such as phosphoglyceric acid may be drawn in one of several directions, according to the reduction potential present, which is determined by the transporters of hydrogen. If these are carrying active hydrogen the acid will be reduced under the influence of light, and the synthesis of sugars will result. If, on the other hand, as in darkness, these transporters are poorly supplied, the acid will be oxidized. In a similar way, the abundance or absence of available nitrogen in the cells leads to a predominance of synthesis or of breakdown of proteins.

The physiological balances are regulated both by external factors, such as light and the supply of food-materials, and by internal factors determined by the provision of the cells with biological equipment, catalysts and enzymes. The working of this equipment is dependent on the age of the protoplasm, and as a whole, organs and their cells pass through a metabolic cycle running from birth to death.²² It begins with new cells and the formation of new organs. These take over the flame and ensure the continuation of plant life. Young cells are much better able to synthesize the proteins of protoplasm than are fully-grown cells. In both leaves and roots there is an ageing process characterized by diminishing powers of synthesis and a tendency for breakdown to predominate.

The mineral nutrition of plants

Jean LAVOLLAY

Experiments performed at the beginning of the nineteenth century by N.-T. de Saussure showed that plants absorb the inorganic salts present in their surroundings, and that the composition of their ashes is subject to significant variation 'according to the season, the type of plant and the part of it'. For the first time great physiological importance was attached to the absorption of minerals and to the presence of certain inorganic substances, such as phosphate of lime, in the ashes of all plants. 'There is no reason,' wrote de Saussure, 'for thinking that they can exist without it.'

In a remarkable round-up of the state of knowledge, based more on reasoning than on experiment, Liebig emphasized the importance of autotrophy resulting from the assimilation of carbon dioxide, and drew attention to the nutritional significance of certain mineral elements of the soil whose indispensable nature was clear to him. He considered that the presence of a chemical element in all plants indicates a physiological need for it.

An enormous amount of analytical research was inspired by this idea, which was later extended, by the work of Gabriel Bertrand and his school, to chemical elements present only in traces in plants. Improvements in chemical analysis have made it possible to detect and even to measure some of them in all species, grown on the most varied types of soil. Their invariable presence and relative concentration in certain organs, which are physiologically very active, indicate the useful purpose of these elements.

The basic elements entering into the composition of the molecules of fundamental organic substances (carbon, hydrogen, oxygen, nitrogen, phosphorus and sulphur) are thus accompanied, in 'vegetable matter', by other elements that have no obvious link with organic substances, but nevertheless appear

essential to plant life. Some of them, such as potassium, calcium, magnesium, sodium, silicon and chlorine are relatively abundant; others such as iron, manganese, zinc, copper, molybdenum, boron, barium, strontium, rubidium, etc, are present only in small or very small quantities. The number of trace-elements regularly found in plants is steadily increasing, and appears to be limited only by the sensitivity of methods of analysis.

In order to discover which of these simple substances are really indispensable to plants, a more direct method was developed in the middle of the nineteenth century. In the first experiments performed by Salm Horstmar, plants were grown without soil in vessels of wax or of glass lined with wax, and fed on a complex salt solution. Omission of certain constituents from the saline mixture and comparison of the plants' growth in the differing media showed the necessity for nitrogen, phosphorus, sulphur, potassium, calcium, magnesium, silicon, iron and manganese.

Later, Raulin applied this method in studying the nutrition of a heterotrophic mould, *Aspergillus niger*, and showed that the mineral needs of this plant are similar to those of autotrophes. When, however, all impurities had been removed from the medium, the

⁽¹⁾ Iron is thus the central element of the organic molecule (haem) which ensures cellular respiration. It is, in this combined form, the active principle of the cytochromes and of cytochrome-oxidase. The enormous activity of this trace-element may be judged from the fact that the cytochromes of 100 grams of wheat-root contain no more than 25 micrograms of iron; and this minute quantity is mainly responsible for respiration.

Little is so far known of the reasons why copper is essential, except that it is this element which is the active principle of several oxidative enzymes whose physiological significance is not yet well understood. As for

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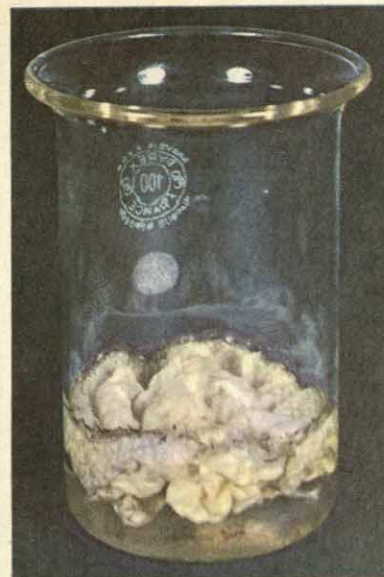
Zn: 0



Zn: 0.25 µg



Zn: 1.25 µg

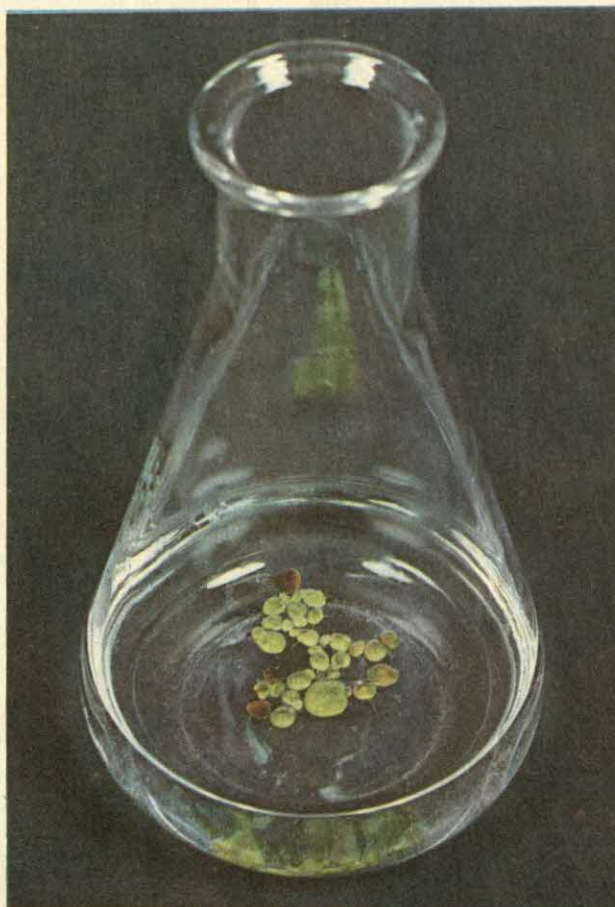


Zn: 6.25 µg

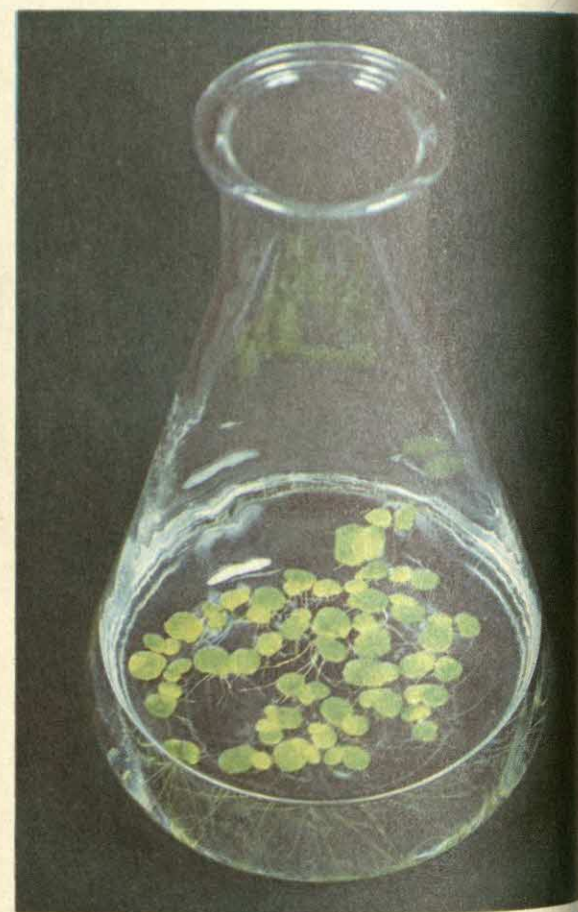
Left: Javillier's experiment showing the need of Aspergillus niger for zinc. The purified medium has been enriched by the addition of varying quantities of zinc, from 0 to 6.25 thousandths of a milligram per culture (0.25 mg per 100 ml).

Right: the same experiment, but an organic substance capable of binding zinc has also been added to the purified medium. The trace-element is not utilized so easily.

Iron and chlorine deficiency in Spirodela polyrhiza grown on a purified medium (after G. Martin). Chlorine is essential for the growth and multiplication of the fronds, and also has remarkable effects on the development of the roots. Restriction of iron reduces the chlorophyll pigmentation (iron chlorosis).



Chlorine: less than 1 µg per 100 ml Normal iron: (100 µg)



Chlorine: 5 µg per 100 ml Normal iron: (100 µg)





Zn: 0



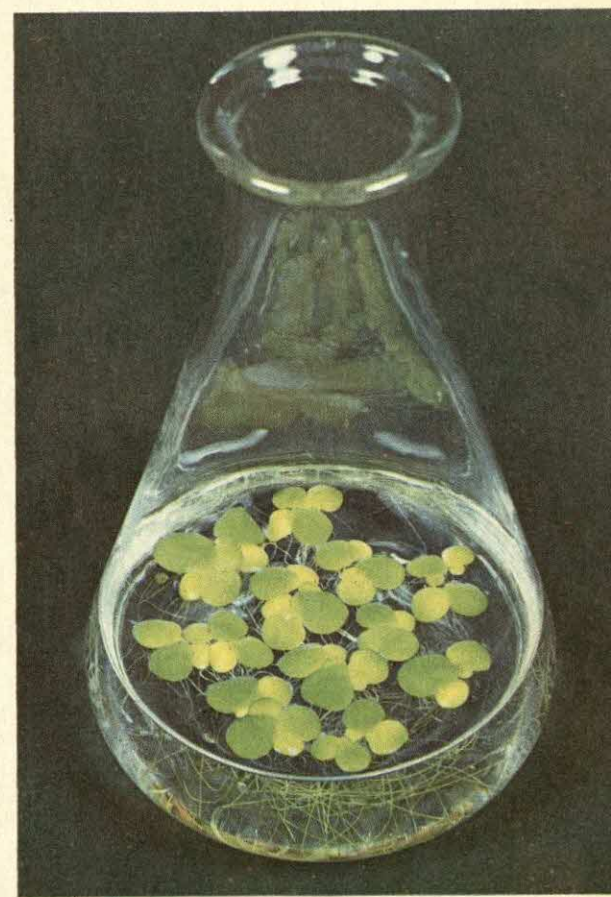
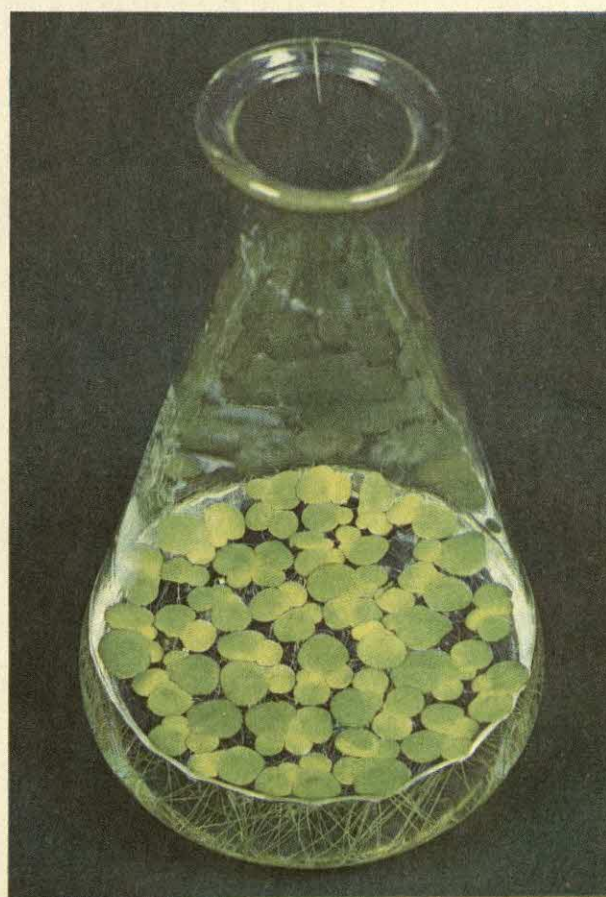
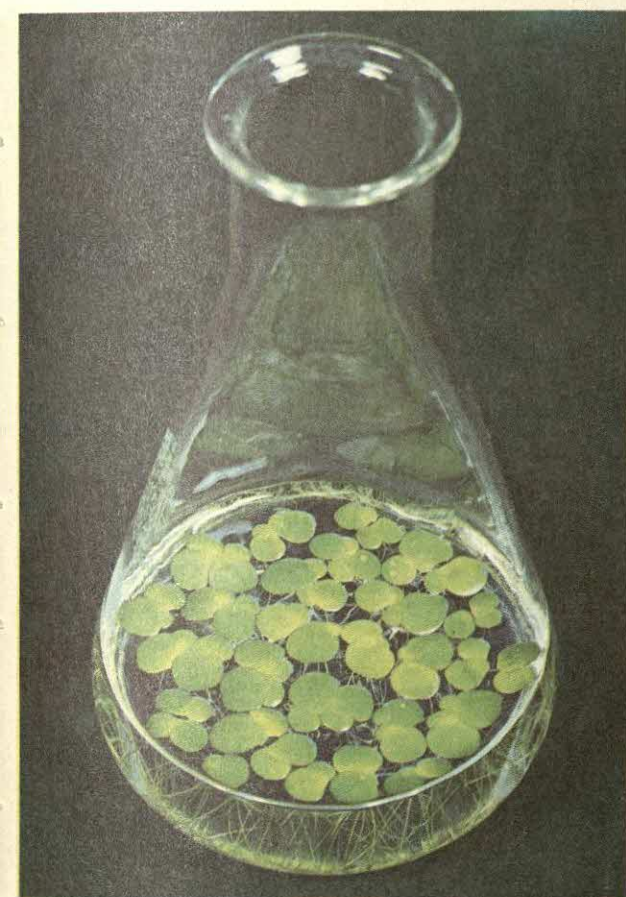
Zn: 0.25 µg



Zn: 1.25 µg



Zn: 6.25 µg



Normal chlorine: (50 µg) Normal iron: (100 µg)

Normal chlorine: (50 µg) Iron: 5 µg per 100 ml

Normal chlorine: (50 µg) Iron: 1 µg per 100 ml

manganese, of which plants sometimes abstract excessive quantities from the soil, it is an element of which minute amounts can activate a whole series of enzymes catalyzing various types of reaction.

Molybdenum is the essential trace-element for the enzymatic mechanism for the reduction of nitrates. In its absence, the very first stages of the reactions that enable plants to use the soil nitrates for synthesis of their nitrogenous compounds, are halted.

Zinc appears to be involved in the biosynthesis of enzymes and hormones; boron in the transport of carbohydrates; and chlorine in an essential stage of photosynthesis. However, the exact mode of action of these elements at molecular level is unknown.

Structural abnormalities resulting from deficiencies are much better known. The visible symptoms resulting from the omission of an element, in experiments of growth on purified artificial media, are easy to reproduce, even when the total composition of the medium is changed. In this way it has been possible to recognize them in plants growing under natural conditions, and to relate them to the same causes.

Deficiency of a particular trace-element can involve the plants of an entire region. For example, in large areas of Australia, there are plants which are more or less deficient in molybdenum. Deficiencies of boron are often seen in crops of beetroot and lucerne, and also in orchards. It appears that zinc deficiency may be equally common. However, unless they are very poor, soils generally contain all the necessary elements, and deficiencies are rather the result of the absence of compounds utilizable by plants.

Deficiency states may also be due to an excess of assimilable forms of other elements, by reason of phenomena of competition at the time of absorption, or of antagonism, the study of which is proving both interesting and fruitful.

growth was greatly increased by the addition of zinc. An additional element had proved of value, and it was found that a very small amount of zinc caused a great increase in the growth of the mould. Javillier showed that the culture medium could be made completely sterile by the elimination of its traces of zinc, and he established a relationship between the concentration of zinc in the medium and the weight of the product. This was the first experimental demonstration of the necessary character of a trace-element.

The presence of small quantities of elements (small, but important in relation to needs) that one would like to exclude in the seeds of higher plants is often a source of great difficulty, and it is essential to reach agreement on the criteria of necessity. An international conference of specialists in 1955 accepted the essential character of carbon, hydrogen, oxygen, nitrogen, phosphorus, sulphur, potassium, calcium, magnesium, iron, manganese, zinc, copper, molybdenum and boron. The need for chlorine as a trace-element then seemed probable and has since been confirmed, bringing the number of elements considered essential for all green plants to sixteen. But, as the precision of chemical and physiological methods progresses, it is probable that in time other trace-elements (eg sodium, vanadium) will be recognized as essential. Certain heterotrophes have slightly different needs: for instance, *Aspergillus niger* does not appear to require calcium, boron or chlorine.

Carbon, hydrogen, oxygen, nitrogen, phosphorus and sulphur are essential constituents of the organic molecules that make up the basic materials of cells (mainly carbohydrates, fats and proteins). The other essential elements fall into two groups corresponding to different quantitative needs. Potassium, calcium, magnesium and even sodium are present in fairly large amounts in plants. As Liebig observed, even when the relative proportions of these elements vary according to the composition of the soil, the sum of their basic equivalents remains relatively constant per unit weight of dried plant. These elements fulfil an important physiological function in balancing acid substances, for an acid-base equilibrium seems just as necessary to plants as it is to animals. Basic elements are, however, only interchangeable within limits, for there is a minimum requirement for each of them. Potassium plays an important part in the osmotic properties of cells, but it must be balanced by its antagonists, calcium principally, and magnesium.

These macro-elements also have specific functions. The most remarkable is the direct participation of magnesium, the central element of the chlorophyll molecule in photosynthesis. Magnesium is also concerned, in smaller quantities, as the essential activator of several biological catalysts (enzymes) necessary for carbohydrate metabolism and controlling the vital functions of photosynthesis and respiration. Calcium in minute quantities is sometimes important, as is instanced by the very small concentrations of this element when acting as a growth factor for green algae or for roots.

The very small quantities in which trace-elements occur make it doubtful whether they can have any function other than to ensure the functioning of enzymatic systems.¹

During the last hundred years, knowledge of the principal requirements of plants grown in artificial media has made possible the partial substitution of mineral for organic fertilizers, whose exclusive use was becoming prohibitively expensive. This knowledge has increased the output of agriculture and allowed the population to multiply. But incomplete knowledge of nutritional needs has limited the use of chemical fertilizers to nitrogen, phosphorus and potassium compounds, calcium being provided by the admixture of lime. By a lucky accident, the use of superphosphates and manure furnished sulphur, magnesium, and trace-elements in variable amounts.

Complete satisfaction of all the mineral needs of crops is not only essential for high yields, but is also necessary for the complete development of all the powers of biosynthesis of organic compounds, and consequently the food-value of plants. In so far as plants are also the only source of inorganic elements, equally indispensable for both animals and man, the presence of sufficient quantities of these elements in edible plants is necessary for our health. An example of this is cobalt, whose significance in the life of cultivated plants is not yet known, but whose importance to man, in the form of vitamin B₁₂, is considerable.

The fear has often been expressed that the use of mineral fertilizers to obtain larger crops involves a decline in their food-value, but surely all the efforts of research are tending towards a better understanding of the needs of plants. It seems absurd to suppose that living organisms could be made unhealthy or even poisonous by adapting their nutritional conditions to their needs.

Elaboration of a plant in vitro



*Culture of
tobacco-stem
tissue with
growth
substances.*

The culture of plant cells and tissues

Albert C. HILDEBRANDT

(1) Agar: gum extract from a marine alga.

(2) Callus: accumulation of cells that form on the wounded surfaces of animal or plant tissues.

(3) Parenchymatous cells: cells with thin walls which are little differentiated and have no specialized functions.

(4) Cambial cells: cells from the zone of intense cellular division which is found inside stems and roots.

(5) Phosphorylation: process by which a molecule of phosphoric acid combines with a sugar and transforms it into a highly reactive product in the chain of chemical reactions.

(6) Clone: population of individuals, or individual cells derived from other tissues by vegetative propagation.

The isolation of living cells of higher plants and their growth and development in liquid or on agar¹ media in glass containers, or on glass slides, has long held man's interest and imagination. The methods now successfully established have provided important tools for the study and clarification of many fundamental biological phenomena.

Callus² cultures may be made from different tissues, stem, leaf petiole, or root. The method of developing such a callus culture is carried out under aseptic conditions.

Macroscopically, the undifferentiated tissues commonly appear as smooth or lobed masses that may be either firm or soft to the touch. As callus tissue they consist largely of parenchymatous cells,³ but in cross-section may be seen to contain, depending on the particular species and source of tissue, varying amounts of vascular tissue and cambial cells,⁴ and various degrees of organization of these components. Differences in rates of growth, pigmentation, development of chloroplasts, softness or firmness, may also be observed depending on the species, the source of the tissue and on the composition of the medium.

The influence of the chemical and physical environment on growth of callus tissue has been extensively studied. Mineral salts, sugars, and growth substances are required. The source and concentration of carbon and nitrogen are critical items for growth or failure of growth. The mineral salts should contain potassium, phosphate ions, sulphur, magnesium, calcium, and traces of iron, zinc, boron, copper, magnesium, and

chlorine ions. The concentration of sucrose for growth of the same species has a critical effect. Cultures are favoured by an acidity of from pH 5.5 to 6.5.

If liquid media are used to culture the callus tissue, some form of aeration is desirable. This may be accomplished by agitating the cultures on a reciprocating shaker, by rotating the culture tubes so that they are exposed to air during part of the cycle, by stirring the cultures, or by bubbling sterile air through the medium. Liquid shake cultures have been routinely used for over 18 years. Liquid cultures of higher plant tissues are commonly started from established cultures growing on agar.

Callus cultures

The success of the method of growing isolated tissues on agar or in liquid media suggested the application of the method to a variety of basic biological problems. The morphology and physiology of tissue cultures of normal and diseased origins have been extensively studied. Normal tissues that are isolated from stem, leaf, or tuber usually require growth substances as supplements to the basic nitrate, sucrose, mineral salts medium.

Diseased tissues isolated from crown-gall tumours induced in plants by the pathogenic bacterium, *Agrobacterium tumefaciens* differ from the corresponding normal tissues in their requirements for growth substances and multiply in tissue culture on the basal medium only. Thus, by tissue culture, it was seen that between

normal and tumour tissue there is a series of nutritionally definable steps. Recently it has been possible to isolate the mitochondria from normal and tumour tomato-tissue cultures. Crown-gall mitochondria oxidised ascorbic acid more rapidly, but their phosphorylating⁵ efficiency was lower than that of normal tissue mitochondria.

The many studies with isolated tissue from higher plants have emphasized the great variety in potentialities for growth and differentiation that are available. Differences in growth habit and nutritional requirements may be seen in tissues derived from even the same species. In addition, the type and amount of growth may depend upon the physical environment, including whether the tissues are grown on agar or in liquid media.

The differences in the cell types and the relative numbers of different cell types within the tissue masses have indicated that the type and amount of growth in the cultures are in reality the result of the interaction of the many cell components of the mass. The nutritional and physical requirements of such cultures is correspondingly an expression of the average requirements of these component cells. Therefore, to learn the cell requirements for growth, division, differentiation, maturation and senescence, it would be desirable to study the single isolated cells or clones⁶ of similar cells that have been derived from a single isolated cell.

Cultures of isolated cells

The hope of isolating and growing single cells of higher plants *in vitro* has been expressed for many years. Early attempts by Haberlandt (1902) and others were unsuccessful largely because of the choice of cells and the lack of suitable culture media. Before cultures of single isolated plant cells could be successful,

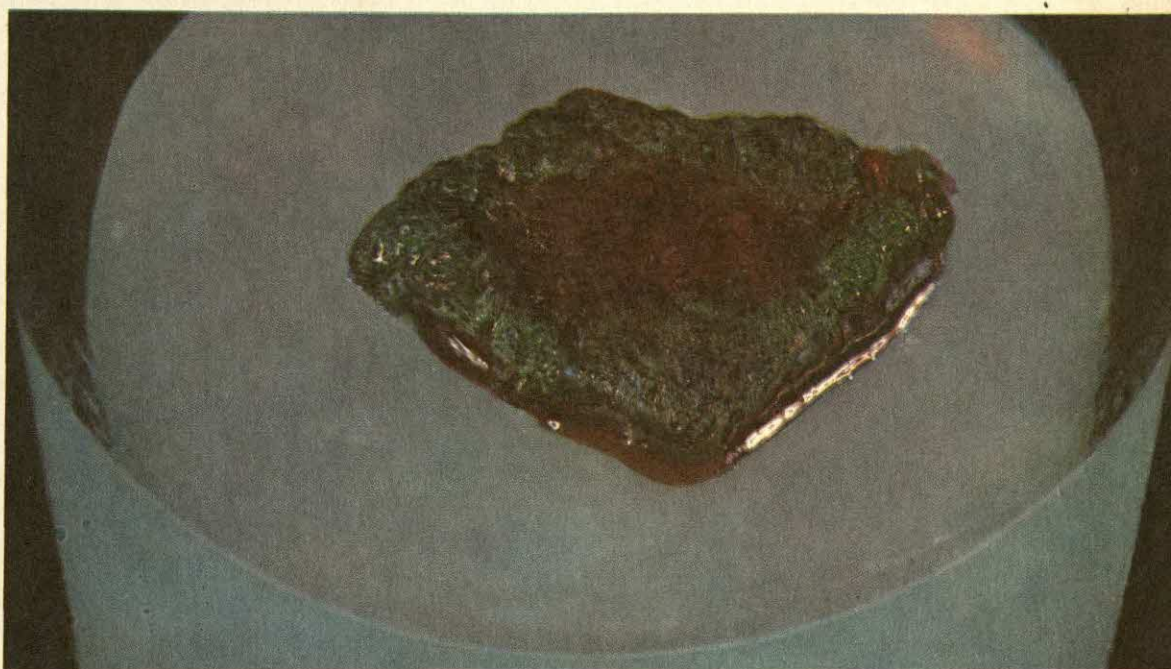


Fig. 1. A slice of carrot in aseptic culture in a test-tube.

Fig. 2. After two weeks, the zones of cellular multiplication appeared at certain points, producing outgrowths that turned green under light. These newly formed tissues were then excised and transferred to a new medium. By carrying out this procedure at regular intervals, Professor Gautheret obtained a block of carrot tissue that is now more than twenty years old (normally the carrot dies at the end of its second year). (Experiment by Nitsch. Photo Lod).

Fig. 3. Tissue culture of Virginia creeper (*Parthenocissus tricuspidate*) transformed by crown-gall. This tumorous tissue was isolated by Dr G. Morel (I.N.R.A., Versailles) more than twelve years ago, and is growing indefinitely in a synthetic medium, deprived of growth substances. (Photo Lod).

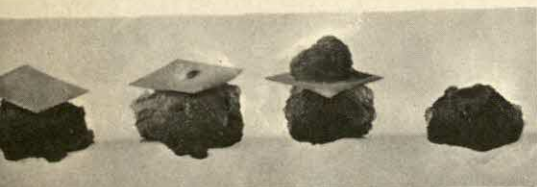


Fig. 4. The 'nurse' culture method of Muir and colleagues for obtaining clones of plant cells from a single cell. Left to right: the 'nurse' culture with a piece of sterile filter paper on top and an isolated cell on it; from the single cell on the filter paper has developed a colony of cells which receives its nourishment from the culture under the filter paper; the new colony is ready to be transferred directly to agar medium. (Photo Hildebrandt).

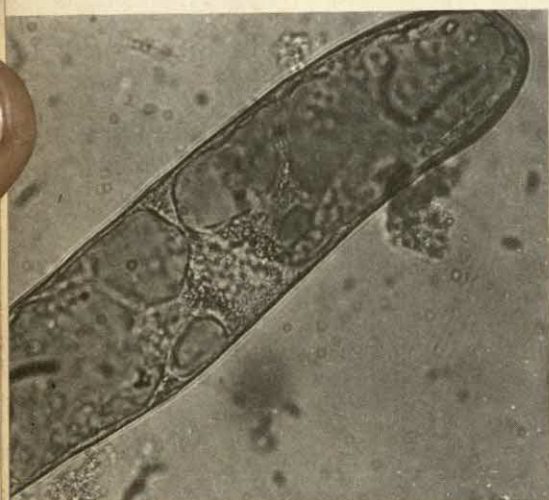


Fig. 5. Chromosomes visible on the living plant cell of tobacco, seen at metaphase. (Photo Hildebrandt).

it was necessary to learn how to grow mixed cell cultures in liquid, or on agar media.

It was first shown possible by Muir *et al.* (1954) to grow clones of tissue from single isolated cells from higher plants *in vitro*. These came from tobacco and marigold cultures. With aseptic techniques, a single cell was picked up under the binocular microscope with a microspatula from liquid or agar cultures, and transferred to an 8×8 mm square of sterile filter paper that had rested several days on an established tissue piece on agar medium. The filter paper with the single cell was then returned to the established tissue piece that then served as a 'nurse' culture. If the single cell was placed directly on the agar medium, it failed to grow. However, the single cell on the filter paper sometimes divided and produced a mass of cells that could be transferred directly to the agar medium where it grew as an established single cell clone. The single cell on the filter paper evidently was exposed to a favourable balance of nutrients and physical condition from the 'nurse' culture. The single cell, filter paper, nurse culture arrangement is illustrated in fig. 4. It was possible to remove the filter paper and cell at any time after placing the cell thereon in order to follow growth of the cell and to ensure that subsequent divisions came from the isolated single cell and not from the nurse tissue. Single cells grew on nurse cultures from either the same or different species. Many single cell clones of tissue from other species were also established by this method.

Single cell clones were secured by Bergmann (1959) by mixing tobacco or bean cells from liquid cultures with agar, plating them into Petri plates and selecting the colonies that subsequently developed from the single cells. Single cells of tobacco were isolated by Jones *et al.* (1960) in a drop of culture medium on a microscope slide, and sealed with paraffin oil and cover slips to provide a micro-culture chamber. The isolated cells were arranged in the micro-chamber in a way that made possible the continued growth and microscopic examination of living, unstained cells. Cultures were kept alive on the slide for months without a change of nutrient. The cells divided and produced masses of cells. Chromosomes are seen at metaphase in fig. 5. Certain cells in old cultures produced several to many cells endogenously. The endogenous cells which escaped through a rupture in the mother cell wall divided and produced normal tobacco tissue masses. Thus the actual division of the single isolated cell and subsequent colony

formation was followed with bright-field and phase-contrast microscopy and recorded with still, motion-picture, and time-lapse photography.

Single cell techniques were used also to study diseased plant growth. Tobacco mosaic virus multiplies at different rates in different single cell clones of tobacco tissue infected *in vitro*. The virus infectivity increases greatly in some clones, moderately in many, and is lacking in others. The clones of tobacco tissue also vary in growth rate, texture, and pigmentation. Certain clones of tobacco tissue are more resistant to infection in a young actively growing condition than are older maturing cultures. One clone of tobacco tissue selected and permitted multiplication of a mild strain of virus when inoculated with a mixture of tobacco mosaic virus strains.

Conclusion

The culture of higher plant cells and tissues *in vitro* has thus opened a new phase of botanical investigation. The method has wide application to many branches of science. The cell or tissue may be grown for unlimited periods on media containing known chemicals, and growth may be observed for weeks without a change of nutrient.

Important breakthroughs already have clarified cell cytology, growth and differentiation and some mechanisms of infection and disease development. Growth and division of single isolated cells can be observed continuously in a drop of medium on a glass slide under a microscope. The action of cytoplasm before, during and following nuclear division can be seen. Single cells can be isolated and grown to tissue masses as clones of tissue, to examine the potentialities for growth and differentiation of component cells in a tissue mass. With certain species differentiation of small masses of cells has been followed through to the production of whole plants.

This new frontier of isolated cell and tissue culture suggests many experiments to clarify basic factors and balances necessary for cell growth, division, and tissue differentiation. Studies of normal single cells and tissue cultures, and those isolated from diseased growths induced by bacteria, fungi, nematodes, and insects, and virus-infected cells may further define differences between normal and diseased cells in terms of common metabolites. Such information may perhaps be used to fashion the key to control diseased growth.

From the organ to the plant

John G. TORREY

Most of us have tried at some time to grow plants from seed, but many plants are not normally propagated in this way. Some we would like to cultivate do not produce seeds in the form necessary for the purpose. Navel orange is a good example. Such plants must therefore be propagated by so-called vegetative methods. Some of us may have tried to grow a plant from the stem cutting of a neighbour's choice specimen, which we have rooted in water and earth. In doing so we have copied a method in use for at least two thousand years. Some 300 years before Christ, the Greek scholar, Theophrastus, wrote about it in his *Enquiry into Plants*:

'All trees which are propagated by pieces cut from the stem should be planted with the cut part downwards, each piece being not less than a hand-breadth in length and having the bark left on it. . . . Some say that the site chosen should be the same as that of the parent tree, facing north or east or south as the case may be. . . . From such pieces new shoots grow; as they do so we should keep heaping earth around them until the tree becomes strong.'

There are ways in which plants reproduce themselves by vegetative means, with or without our interference. With some this is the only method, since reproduction through seeds produced by sexual means does not occur. From our point of view such a method has many advantages. Of these the most important is that the new plant will be, like the parent-plant, stable in all its characteristics. Such stability is not assured by seed-planting, since by genetic variability we may lose the very character we wish to preserve.

In nature, vegetative propagation results from several methods, such as the rooting of stems from tillers in the grasses and cereals, or the production of runners we see in strawberries. Some plants use a variety of propagules—that is, bits and pieces. For example, Irish potatoes are grown from pieces with eyes; these are dormant plant shoots which can be used to grow whole plants. In some cases, root pieces develop buds, as for example, horse-radish. Others develop buds on leaves;

anyone with 'green fingers' can, for example, grow an African violet by placing a leaf with its base or petiole in water or earth.

In all such propagations we are taking advantage of the unique regenerative capacities of plants to produce a whole from an isolated part. Only in the past twenty-five years have we begun to understand the mechanism that lies behind these capacities.

In 1934, the first plant hormone was isolated and differentiated chemically; this was 'indoleacetic acid' (see the chapter on 'Plant Hormones'). It is one of the class of compounds called 'auxins', so named because they have the power to stimulate stem elongation. Among many of the interesting actions it shares with other compounds that are closely related to it chemically is its power to stimulate the formation of roots on root pieces and on other isolated plant parts, but especially on stem pieces. Part of this power is the ability to stimulate cell divisions in certain of the plant tissues that lead to new root structure. Here we have the explanation why stem cuttings root better when they have an attached leaf or bud; the auxin is formed in these attachments, and when the cutting is made, it moves to the base of the stem. It follows that rooting from stem cuttings can be assured by applying auxin to their bases.

Auxin effects bud elongation but cannot make plant parts produce buds; apparently something else is necessary. Yet it gives us a clue to the control that lies behind the regeneration in plant systems; it is hormonal control. As it is difficult to study these hormonal controls in complete plants, botanists now concentrate on the study of the behaviour of isolated parts. This study has, however, its own intrinsic problems and many botanists working on tissue culture *in vitro* have become fascinated with the technique rather than with its use to produce knowledge of the part played by hormones in regeneration and behaviour.

In 1939, in the United States, Dr P. R. White reported the growth of isolated roots of tomato, 'Lycopersicon', in a synthetic nutrient medium, and showed that the culture could

The picture on page 35 shows Professor Skoog's experiment. Tobacco stem needs both a kinetin and an auxin in order to proliferate. At the start all the fragments were of the same size. The photograph represents (from right to left) the fragments placed in the following media at the end of the experiment: basic medium; basic medium plus 6-furfurylaminopurine (0.1 mg/l); basic medium plus indole-3-acetic acid (1 mg/l); basic medium containing both substances. (Experiment by Nitsch. Photo Lod).

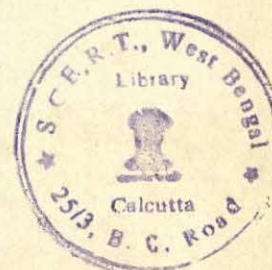


Fig. 1. Two days after pollination, the ovary of the tomato is separated from the plant and planted in the test-tube in aseptic conditions.



Fig. 2. Under the influence of the nutrient elements of the jelly, the ovary grows.



Although no one has yet made babies in test-tubes, more than ten years ago Nitsch developed fruits in vitro from isolated flowers like those of the tomato. (Experiment by Nitsch. Photo Lod).

apparently be maintained indefinitely. His first cultures were from half-inch root tips cut from seed plants grown under sterile conditions in the dark; the sugar in the medium

was two per cent sucrose, mixed with mineral salts and several vitamins, including thiamin and pyridoxine. The isolated roots did not need added auxin; apparently they made their

Fig. 3. The ovary ripens under light.

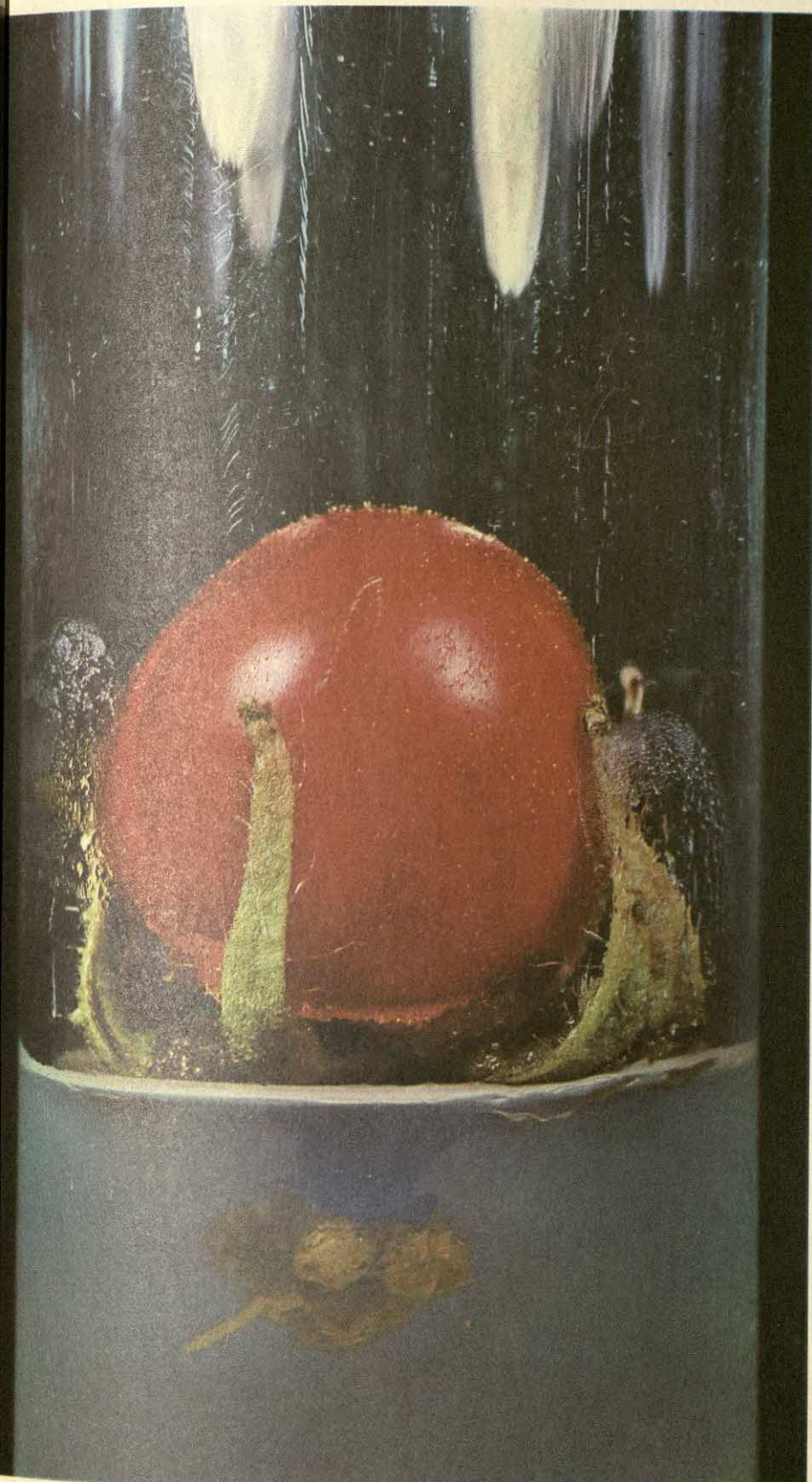


Fig. 4. In the dark, the ovary remains white and a number of adventitious roots develop on the peduncle.



own. They looked and behaved much like whole-plant roots, growing about an inch a day and branching profusely. Root tips or segments could be transferred to fresh medium

in a few weeks. Continuous culture from the same root was maintained for over twenty years and seemed to suffer no deterioration after well over 1,000 transfers. Many similar

experiments have since been carried out with a wide variety of plants, and White's medium has been found to meet the needs of the isolated plant roots.

White's excised tomato root is an example. In the first culture it required, for energy and carbon, the sucrose in the medium. In the intact plant the root gets its sugar from the green leaves, in which it is made by photosynthesis; they cannot make their own, even when exposed to light, as they lack the necessary chlorophyll pigment, present in leaves. Like the whole plant, they need certain minerals for the maintenance of cellular machinery in the protein structure of the plant body, as catalysts in enzyme reactions, as cementing material for cell walls, and as osmotic agents. Their essential vitamins, which are also made in the green parts exposed to light, are transferred downwards in minute quantities. By learning the requirements for such isolated cultures we get to know their possession or lack of synthetic powers, and the interdependence of root and shoot.

Isolated tomato roots cultured in White's medium do not produce shoots; what they lack in order to do so we do not yet know, but by varying the environmental and nutritional conditions we may find the answer.

An interesting parallel is the culture of the isolated roots of the common weed-pest, convolvulus, or morning glory. They grow rapidly and have been maintained continuously in regular subtransfers for over five years. The medium used is relatively simple; it contains sugar, mineral salts and the B vitamins thiamin and niacin in low concentration. What is interesting about these roots is their ability to form spontaneously both branch roots and shoots. *In vitro* it is possible to prevent bud development, but we now know why this weed flourishes naturally, for the more the root is broken up, the more it produces whole plants. By using organ and tissue cultures we may find what it is in its internal chemistry and physiology that gives such a capacity for regeneration.

Many attempts have been made to discover the inherent characteristics of other plants by such culture methods. In our laboratories Dr Al-Talib has been studying the growth of the terminal bud of the Douglas fir tree. He was able to excise it in its dormant winter-period, sterilize the surface, remove the bud scales, and cultivate it with all its tiny leaves already formed for the next year's growth. On a medium containing the sugar which young buds cannot make, mineral salts,

and other growth factors such as vitamins, many of the leaves grew to full size although the bud itself did not elongate as it would have done on the whole tree. Development seemed to be improved, however, when organic nitrogen, in the form of urea and asparagine, was added. Apparently auxins were already present, but it was found impossible to induce root formation in any of the hundreds of cultures. It may be that the absence of the root brings hormonal limitations.

Dr T. A. Steeves and his associates have shown that excised leaves, removed as embryonic structures about 1 mm in length, can be grown to normal appearance if not normal size on a relatively simple medium. They worked with ferns such as *Osmunda* and with higher plants such as the sunflower. Leaves, unlike isolated root tips or shoot tips, whether isolated or attached, reach a given size and then stop developing; their development is therefore described as determinate, as distinct from the indeterminate development typical of the root. When it was possible to isolate the very youngest leaf primordia from the shoot apex in ferns and culture them, leaves were not produced, as is the case with the older primordia, but they developed into entire plants, forming first a shoot and then a root. In these primordia the inherent capacities for total regeneration were present, whereas in the older ones the determinate pattern of development was already fixed. Cultivation *in vitro* may give us some clue to the mechanism of determinate growth and, what is more important, to that of indeterminate growth, which allows complete plant regeneration.

About the same time as White grew successful cultures of excised tomato roots, Professor R. Gautheret in France reported, in 1939, on his success in plant tissue culture. He started with tissues from the large underground root of carrots. Pieces were removed under sterile conditions and grown on a nutrient medium containing sugar, mineral salts, certain vitamins and auxin. At the cut surface they formed callus tissue which could be excised, transferred to new medium, and propagated—apparently indefinitely, as essentially undifferentiated cells. The tissue grew without apparent organization, showing on a synthetic medium neither roots nor shoots.

Such tissues are of particular interest because of their capacity to 'regenerate' complete plants. In culture under these conditions organ initiation is apparently suppressed, but it is nevertheless possible, by changing the

Fig. 5. Just like a tooth erupting, the new root, formed deep in the stem, pierces the outer tissues in order to emerge. Note the alignment of the swellings made by the pressure of other roots in the process of developing. (Experiment by Nitsch. Photo Lod).

Fig. 6. Emergence of adventitious roots on a bean cutting formed from the tissues of an internal layer of cells, the pericycle. In the centre, large cells of the stem. The new roots are disposed along well-defined lines.

physical conditions, or, what is more interesting, by modifying the chemical environment, to induce the initiation of organized structures in roots or buds or in both. This was done with pea root callus, which had been cultivated for over a year as an unorganized tissue mass through many subtransfers before being grown in an appropriate medium. No buds have been produced from this tissue under any of the conditions so far tested.

The most detailed study of organ initiation in callus tissue has been made by Professor F. Skoog, of Wisconsin University. He found that tobacco-stem tissue grown in a sterile nutrient medium could be induced to form roots if treated with the growth hormone indoleacetic acid, an auxin. In these conditions, the tissues were not unlike stem cuttings made to form roots. He also found that when quite small amounts of the purine 'adenine' were added to the medium, bud formation could be induced. The 'adenine' and the auxin were found to be antagonistic to each other, auxin at high concentrations tending to induce roots, adenine in high concentrations tending to induce shoots. When they were balanced in the medium, the tissue grew as an unorganized tissue mass. Adenine is an important constituent in all living cells; it plays a major role in enzymatic systems concerned with their energy exchange, and enters into the constitution of the important nucleic acids which are fundamental to their metabolism. Extra amounts fed to the tissue somehow forced the cells into organized shoot structures. Recently, Miller and Skoog isolated a compound closely related to it which they called 'kinetin'; it is a factor in cell division even more active than adenine in the process of bud initiation. Thus was discovered a new class of compounds, 'kinins', that interact with the auxins in the control of plant development. According to Skoog, it is their balanced interaction which controls the direction in which plant organization will proceed. By their manipulation it may be possible in



the near future to produce whole plants at will and in quantity from callus tissue of mature plant parts grown *in vitro*. Indeed, as our knowledge increases it may become possible as a routine procedure to start with selected single cells, develop callus tissue from them, and then induce bud and root formation that will result in new plants.

Tissue cultures can be maintained *in vitro* for long periods in relatively small space, and this may well be the form of plant propagation of the future, using plant-tissue culture-banks as our sources of supply.

One type of organ culture has already proved useful in agriculture and horticulture. This is the cultivation of isolated plant embryos. Flowering plants reproduce through seed formation after pollination. The union of the germ cells of pollen and egg gives rise to a single cell, which undergoes cell divisions, first slowly and then rapidly, in stages of increasing complexity, from the immature embryo to the embryonic plant within the matured seed. For many different reasons the tiny plant may not develop. In plant hybrids the nutrition is often inadequate, while in some seeds germination is prevented by the enveloping coat. In some cases, natural germination takes many years. For several reasons, therefore, it has been found useful to open the seed, isolate the embryo and transfer it to a nutrient medium, where it grows in sterile conditions into a mature plant in a test-tube. Even quite minute embryos can be dissected and cultured in a nutrient medium until mature and then carried through as young seedlings up to mature plants. The classical material used to demonstrate this process in the teaching of botany is the embryo of the common weed, *capsella*, or shepherd's purse. The embryo, starting as a single cell, forms by cell divisions a spherical mass of tissue, known as the globular stage. Then by cell differentiation, early organ formation begins with the development of cotyledons in the heart stage; later comes elongation of the axis with development of shoot and root ends in the torpedo stage, which contains the basic structures of the whole plant. In the mature seed, the embryo is bent in half and enclosed in the seed coats.

Isolated embryos of the torpedo stage can be brought to maturity on a relatively simple nutrient medium. Heart-shaped embryos have more elaborate nutritional needs, and globular ones still more complex needs; very small ones have not yet been cultured successfully. The single-celled embryo, the omnipotent cell *par*

excellence, has yet to be isolated. The progressively more complex nutritional needs of progressively younger embryos are reflections of the different synthetic capacities of the developing embryo. Even so, much practical usefulness has resulted from the culture of immature embryos in a variety of important agricultural and horticultural plants, including stone fruits, certain forest species, and, in particular, desirable hybrids which would never otherwise be brought to maturity.

During 1959, plant tissue culture and embryo culture met in an interesting and exciting way which shows their common problems and their important potentialities. For several years Dr J. Reinert, of Germany, had maintained a carrot tissue culture on a complex nutrient compound, in which it grew rapidly to an essentially undifferentiated tissue mass. In studying the tissue's capacity to produce organs under various experimental conditions, he transferred it to different nutrient media; first, for several weeks, to an elaborate synthetic one, then to this medium without auxin, and finally to a complex one. From these callus tissues he grew whole plants with roots and shoots. When he examined the tissues and cells in detail at every stage of development, he discovered within the undifferentiated cellular mass the production of many true bipolar embryos, just like those that normally develop only in the seed; in other words, he had induced the typical developmental stages usually associated with sexual reproduction, and this he had done by vegetative means with all the advantages of a stable system and without genetic variability. If this is possible with carrot tissues, we may soon be able to devise simple procedures for the production in quantity of our most desirable horticultural and agricultural plants.

The significance of this development is most easily seen by considering the parallel in animal tissue culture. Biologists are now able to cultivate animal tissues and cells on much the same lines. Cultures of human skin cells and muscle cells are now routine procedure. Let us suppose that by varying the constituents of the medium, we could start with a suspension of relatively undifferentiated cells, such as fibroblasts, and induce them to organize embryonic structures *in vitro*; this would indeed be a remarkable accomplishment. It may prove to be impossible, but the similar process is possible with plants. Future developments of these studies may well bring a remarkable change in our methods of plant production.

The variety of the plant world



*The curious
flower of
Cypripedium.
(M. Vacherot,
Boissy-Saint-
Léger,
France.
Photo Lod).*

The abundance of plant forms

Marius CHADEFAUD

A glance at the vegetable kingdom as a whole is enough to reveal that it consists of an astonishing range of species, from unicellular algae to the trees of our forests. By their size, external form and internal structure, the variety of plants appears at first sight to be almost infinite, and one wonders if there is any way of classifying them. It has, however, proved possible to do so, and if we confine ourselves to a broad outline we find on analysis that this variety is the expression of a limited number of patterns, liberally modified by the process of evolution.

(1) Protocaryote types: from the Greek 'protos', first, primitive, and 'karyon', nut, nucleus. This term is used to describe organisms whose cell nuclei are still very imperfect and primitive.

(2) Eucaryote types: from the Greek 'eu', good, and 'karyon', nut, nucleus. This term describes organisms whose cell nuclei are perfectly individualised.

(3) Thallus: from the Greek 'thallos', young shoot.

(4) Bast: the tissue in plants which contains the nourishing sap elaborated in the leaves. In trees, it forms the internal part of the bark, and it may be laminated like the leaves of a book.

There are two main cellular patterns among plants. There is, first, that of blue algae, with imperfect cellular development, ie the protocaryote¹ group, which do not have proper cell nuclei: chromatin, the essential nuclear substance, certainly exists, but it is not located in definite nuclei; and there are no chloroplasts or mitochondria. The second, or eucaryote² group, comprises the other algae, fungi, and all higher plants, whose cells are fully developed with true nuclei, chromatin in chromosomes, mitochondria, often with chloroplasts, with or without chlorophyll.

From a structural point of view, there are more varieties. We shall examine in turn examples of algae (blue, green, brown, and red), fungi, and higher plants.

Algae and fungi are Thallophyta. Their vegetative apparatus, or thallus,³ sometimes consisting of only one cell, carries neither roots, leaves, nor flowers, and has no well-differentiated tissues such as the wood (xylem) and the bast⁴ (phloem), in which the sap circulates in higher plants. In contrast, the vegetative part of higher plants such as mosses, ferns and flowering plants is the cormus,⁵ a much more complicated organ, bearing in general leafy branches, often also roots, and well-differentiated tissues such as wood and

bast. These plants are therefore known as Cormophyta, and may be divided into those which, like the Thallophyta, lack flowers (Cryptogams Cormophyta, such as mosses and ferns), and those with flowers (Phanerogams Cormophyta, such as pines, buttercups, lilies, oaks, etc).

The thalli of algae

In algae, the thallus has chlorophyll, giving it a green colour (green algae) unless masked by other pigments (blue, red, and brown algae). From the anatomical point of view it nearly always takes one of three forms: a group of several cells, a syncytium (without intercellular walls), or a single cell.

Multicellular types

(a) The simplest is the bundle of cells (or archethallus). It originates from a single cell, which divides into two daughter cells, then four, eight, sixteen, etc, which remain joined together. It may be globular, cuboid, tubular or irregular in shape. It multiplies by breaking up into smaller bundles, or even into separate cells. It can also reproduce by spores⁶ or by gametes.⁷ Its cells then become 'sporocysts'⁸ whose contents divide up into spores; or 'gametocysts',⁹ which likewise give rise to male

and female 'gametes'. Both spores and gametes are set free; they are reproductive cells. Every spore grows and itself becomes the first cell of a new thallus. Gametes, on the other hand, join together, one male to one female. From this union results an egg-cell (zygote) which, like a spore, gives rise to a new thallus (or, as sometimes happens, transforms itself into a sporocyst, which breaks up into spores; then it is the spores that form the new thalli).

(b) Next comes the simple filamentous type (or linear archethallus): a thread without branches, which lengthens by transverse division of its cells.

(c) The branching filament (or protothallus) is more complicated. When fully developed it consists of two kinds of thread. Some lie flat on the substratum, on which they branch. The others, arising from the former, stand up at right angles to the substratum, and they also ramify. Sporocysts and gametocysts are usually borne by the upright filaments. But there are many variations: the threads may all be horizontal, or there may be a single vertical one which in certain species branches but which in others has lost the power of ramification.

Whether horizontal or vertical, the filaments branch by the budding-off of lateral daughter filaments, which are often telomic.¹⁰ They lengthen by transverse division, not of all their cells, but only of the few cells (often a single one) that constitute their growing point. This is usually at the tip (apical growing point), but may alternatively be situated intermediately (intercalary growing point).

In certain species, the filaments of the thallus form columns, tubes, bands, plates, or sacs, by the division in various directions of the cells composing them.

(d) Even greater complexity is seen in the group of cladus¹¹ or branched thalli. This term indicates systems composed primarily of a main strand, or axial filament, which lengthens indefinitely, and whorls of lateral branches with limited growth (Chadefaud's 'pleuridian whorls'),¹² which remain short and some or all of which may grow up and down the axial filament, forming a cortex enclosing it. These various filaments are often telomic, and sometimes develop by further cell division into columns of varying thickness, tubes, plates, stalks, etc. The whole plant is not unlike the leafy branches of a cormus: the axial filament is comparable to a stem, and the pleuridian whorls, usually well supplied with chlorophyll and therefore assimilatory in function, sometimes deciduous, resemble leaves. Sporocysts



Fig. 1. Dichotomous thallus of a liverwort, *Marchantia polymorpha*, bearing propagula, little groups of green cells whereby the plant reproduces vegetatively. (Photo Lod).

and gametocysts are formed on the pleuridian whorls.

In any case, the thallus consists of one or more primary cladi, from which secondary cladi arise, and they in their turn produce tertiary cladi, etc. Each cladus originates in place of a pleuridian whorl, or at its base.

(e) Finally, there is the fucoid pattern (seen in brown algae of the genus *Fucus* and other genera), which seems to be derived from (d) by transformation of each cladus into a complex column or band. The pleuridian clusters are completely incorporated in it, and instead of branching laterally, it divides by successive bifurcations (dichotomy).¹³ This pattern occurs only in the more advanced species, but it is the result of a simplifying regressive type of evolution, in contrast to the progressive evolution of rhodomeloid¹⁴ cladi characteristic of red algae.

Siphonate and unicellular patterns

(a) A certain number of green algae, of the branching filament or cladus types, are siphonate:¹⁵ their thallus is not divided into cells. It has an outer wall of carbohydrate, and the protoplasm within nearly always contains

(5) Cormus: from the Greek 'kormos', stem. A vegetative apparatus consisting of stems, which generally bear leaves, at least when young.

(6) Spores: from the Greek 'spora', seed. Microscopic germs, generally unicellular, of algae, fungi, and other cryptogams. They may be motionless, or able to swim freely with the aid of cilia, which act like oars. Not to be mistaken for seeds.

(7) Gametes: from the Greek 'gamos', marriage. Cells generally resembling spores, but of male and female varieties, whose function is to unite in pairs (one male to one female gamete) to form fertilized egg-cells.

(8) Sporocysts: vesicles in which the spores of algae and fungi are formed.

(9) Gametocysts: vesicles in which the gametes of algae and fungi are formed.

(10) Telomic: from the Greek 'telos', end. This term is used to describe an elementary organ, usually elongated, and growing in length as a result of the activity of a growing point, which is generally at its tip. A root, a stem, every vein of a leaf, are telomes: their tips are the multiple extremities of the vegetative apparatus.

(11) Cladus: from the Greek 'klados', branch.

(12) Pleuridian whorl: from the Greek 'pleuron', side. A whorl of filaments constituting lateral branches of limited growth on the side of the vegetative axis of an alga.

(13) Dichotomy: division by bifurcation.

(14) Rhodomeloid: resembling the red (marine) algae of the genus Rhodomela.

(15) Siphonate: term applied to filaments or vesicles forming the vegetative apparatus of algae and fungi, when they are not divided up into cells by internal walls.

(16) Coccoid: from the Greek 'kokkos', seed, pip. This term describes the non-swimming unicellular algae consisting of a coated cell, often round or oval, shaped like a seed.

(17) Chlamydate monadic: from the Greek 'monas', unity, and 'chlamys', tunic. Algae are called monadic when they consist of a single free-swimming cell, and chlamydate when this cell is 'clothed' in a tunic, the cell wall.

(18) Hyphae: from the Greek 'hyphe', tissue, cobweb. The filaments of fungi, when they are divided up into cells.

numerous nuclei which are not separated by cell walls.

(b) Several other algae, mostly green or brown, are unicellular, their thallus being reduced to a single cell of microscopic size, which may be:

—provided with a cellulose and immobile wall (coccoid type),¹⁶

—with a similar wall, but able to swim with the aid of cilia (chlamydate monadic type),¹⁷

—similarly able to swim, but naked, without any cellulose wall (naked monadic type).

These unicellular algae are of two kinds. The first are related to the primitive 'clump of cells' type, from which they differ only in that the cells do not stay joined together but become each a distinct unicellular individual. The second may be derived from more complex types, by reduction of the thallus to its parent-cell, which becomes a sporocyst or a gametocyst directly. Each spore or egg-cell then becomes the single cell of a new thallus.

Unicellular algae resemble the spores (which may or may not be mobile) of the multicellular species to which they are related. The naked monadic types lead to the protozoa, and thus the animal kingdom, into which they could develop by ceasing to form chlorophyll and acquiring the power to eat and digest solid food; certain protozoa are thus related to some of them.

The thalli of fungi

The vegetative apparatus of a fungus is usually a branching filamentous thallus without chlorophyll, known as a mycelium. Its threads are either in the form of hyphae,¹⁸ each divided into a single row of cells, or of multinucleated siphons without any division.¹⁹

(a) The divided mycelium types are essentially the Ascomycetes (pezizae, morels, truffles, etc, which produce their spores in sporocysts called asci)²⁰ and the Basidiomycetes (mushrooms, toadstools, etc, whose asci become basidia,²¹ with horns or sterigmata, at whose tips the spores form). Their mycelium probably originates as follows. In certain microscopic Ascomycetes that live on insects, the Laboulbeniales, each spore gives rise to a tiny cladus, which is sometimes fixed to the host by 'rhizoid filaments' at its base. In the other Ascomycetes, and in the Basidiomycetes, the cladus atrophies. Only the rhizoids develop: they become very long, ramify, and constitute the mycelium. The fruits of all these

fungi, both edible and poisonous, are masses of hyphae with either asci or basidia. Lichens are Ascomycetes or Basidiomycetes living symbiotically with algae.

(b) Yeasts are derived from the divided mycelium type. Their vegetative apparatus consists of globules, unicellular and uninucleated, which multiply by budding. The formation of each bud is accompanied by division of the nucleus; one of the daughter nuclei enters the bud, which becomes a new yeast cell; it may or may not separate from the parent cell. It is clear how this type originated, for in certain Ascomycetes and Basidiomycetes the mycelium or the spores are able to bud off globules similar to those of yeasts, and which form buds themselves.

(c) The siphonate mycelium type is seen particularly in the Phycomycetes, a 'lower' kind of fungus without large sporocysts or gametocysts, whose spores and gametes generally swim freely by means of flagella. In its complete form, this type comprises a globular or vesicular centre, from which grow:

in the substratum, rhizoid filaments;²²

on the substratum, filaments in the form of stolons,²³ on which new centres may form;

away from the substratum, reproductive filaments bearing sporocysts and gametocysts.

But in the majority of species the thallus is incomplete; its centre is indistinct; stolons may be absent; in other cases (for example, several Chytridiales²⁴) it reduces itself, on the contrary, to its centre which buds or becomes a sporocyst or gametocyst itself.

(d) Finally, there is the plasmodial type, seen in Myxomycetes, whose body is a 'plasmodium', ie a sort of giant amoeba, with many nuclei, and having an animal's way of life and nutrition. This plasmodium later becomes a fruit with spores, and its appearance is that of a fungus.

The cormus of higher plants

In the Cormophytes (as in many algae and fungi), certain individuals called gametophytes produce egg-cells; these engender other types of individual, the sporophytes, which bear spores; from them arise new gametophytes, and the cycle begins all over again. In the mosses and liverworts, each gametophyte is a vegetative apparatus; it bears capsules with spores, the sporogonia, which are, in fact, the sporophytes. Among ferns and other vascular cryptogams, and similarly in the phanerogams, the vegetative apparatus is, in contrast, a sporophyte. In all of them, the spores are

formed in complex organs called sporangia, which may be typical in form or greatly modified.

Whether it is a gametophyte or a sporophyte, the vegetative apparatus is a cormus, sometimes with leaves and sometimes in the form of a thallus.

(a) The type of cormus with leaves is formed basically of leaf-bearing branches arising from each other by budding, and each consisting of a stem with leaves and buds. Except in the mosses and liverworts, there are usually also roots.

A leaf-bearing branch is comparable with the branch or cladus of an alga, but its structure is much more complicated. The central part of the stem (the pith, in present-day phanerogams) would correspond to the axis of a cladus. Its external part (in phanerogams, the wood, bast, bark and epidermis) would be comparable with the pleuridian cortex. The leaves are the equivalent of pleuridian whorls, and their veins, which contain wood and bast, are reminiscent of the filaments composing the whorls.

The leafy branches thus constituted must have resulted from a long period of evolution, from the most distant geological past. At first, the cormus may have been formed simply of laterally branching telomic axes, all similar. This hypothetical stage would have been equivalent to that of branching filamentous thalli. Then something analogous to cladi would have developed, with a main axis carrying bunches of secondary pleuridian axes at its sides. From this the typical leaf-bearing branches might finally have developed.

There have been many variations on this theme. In former times, among the most remarkable were the zygopterous ferns of the Primary period, whose leafy branches were borne by a 'primordial rhizome' without leaves, and bore in their turn not only leaves, but 'foliar complexes', each consisting of two rudimentary 'aphlebian leaves', and two 'typical leaves', which were either sterile or furnished with sporangia. At the present time, we know the amazing variety of leafy branches found in weeds, trees, creepers, the suckers of trailing plants, rhizomes, tubers, bulbs, etc.

Of all these varieties, the most interesting is undoubtedly the flower of an Angiosperm, which is a miniature branch whose leaves are: (1) the *sepals*, constituting the calyx; (2) the *petals*, forming the corolla; (3) the *stamens*, bearing sporangia in the form of pollen sacs, from which spores issue, converted into pollen



Fig. 2. Forking into two equal branches is seen in the fossils of some extinct plants, like this *Sigillaria* of the upper Carboniferous period. (Museum of Natural History, Paris).

grains; (4) the *carpels*, forming the pistil, which contains sporangia that are converted into ovules.

The pollen fertilizes the pistil and its ovules, and the flower then becomes a fruit in which the ovules become seeds.

(b) The thalloid or fucoid type of cormus seems to be derived from the above by the reduction of leaf-bearing branches to their stem, on which the leaves are no longer distinct, and which branches by successive dichotomy, like the thallus of a *Fucus*. In the Primary period, this was the pattern of little plants such as *Rhynia*, which had upright branches formed by dichotomy from a cylindrical stem and terminating in sporangia.

At the present day, this pattern is seen in certain liverworts, and likewise in mosses, each of whose branches is a green ribbon dividing by dichotomy and lying on the ground. On the under surface of the ribbon there may still be scales, which are the vestiges of earlier leaves.

(19) Siphons: the filaments of fungi and algae, when they are not divided up into cells.

(20) Asci: from the Greek 'askon', bag. A special type of sporocyst in the form of a sac, in which the ascomycete fungi, such as morels, pezizae, and truffles produce their spores.

(21) Basidia: cells in the basidiomycete fungi such as mushrooms and toadstools, that produce spores by budding and bear them until they break off.

(22) Rhizoids: from the Greek 'rhiza', root. Filaments resembling roots, in algae and fungi.

(23) Stolons: creeping branches like the runners of a strawberry plant. Trailing filaments of algae and fungi similar to such runners.

(24) Chytridiales: a group of microscopic fungi, mostly unicellular and parasitic on algae.

Table of the plant world

THALLOPHYTA
without tissues

BRYOPHYTA
with tissues



*algae,
fungi,
lichens*



*mosses
liverworts*

Non-vascular plants

Vascular plants

VASCULAR CRYPTOGRAMS flowerless

PHANEROGAMS with flowers



*ferns,
horsetails,
club-mosses*

*resinous trees,
gingko*



GYMNOSPERMS
with naked seeds

ANGIOSPERMS
with seeds enclosed within the fruit

Monocotyledons

plants with striped leaves, eg yucca; perennial plants with a rhizome, eg iris; bulbs, eg lily, hyacinth; and annual or biennial plants, eg cereals, graminaceae.



Dicotyledons

all non-resinous trees, eg oak, lime, lilac, coffee-tree; herbaceous perennials, eg lucerne, dahlia, compositae; biennial plants, eg beetroot, chicory; and annuals, eg peas.



Classification of the plant world

Louis EMBERGER

Classification, or systematization, is the assembly of facts into a single body of knowledge. Every classification rests on the features and properties of the objects being compared, determining similarities and differences, just as on the choice of a method, to allocate to each of the characters its proper value. When it is a question of organisms that are living or have lived, the only natural classification is that which explains their descent, and consequently, phylogeny.

Unfortunately, the relative rarity of fossils and the extreme slowness of phylogeny make it impossible to observe this process directly, so that the deductions made are derived from comparisons. It follows that in every classification, however natural it may aim to be, there is an objective element, denoted by the characters of the objects studied, and also a more or less subjective part, which consists of attaching degrees of importance, ie establishing a hierarchy or a subordination of the characters.

Since direct observation of phylogeny is impossible, it is clear that in order to meet this deficiency and to minimize errors, we must acquire as complete a knowledge as present science allows, of the objects to be classified, for a negligent or imperfect appreciation of a single feature may make a fundamental difference to the classification.¹ Michel Adanson (1727-1806) was the first to enunciate the principle that we must possess a complete range of the characters to be classified, if our deductions of affinity are to be as exact as possible. Furthermore, application of the principle laid down by Antoine-Laurent de Jussieu (1748-1836) of the subordination of observed characters must lead to the correct expression of natural relationships between the objects classified.

Now let us see how these fundamental principles may be applied to the classification of organisms that have lived or are now living,

taking the plant world as a case in point.

The description of species

Knowledge of plants, whether fossil or living (for the past cannot be separated from the present), is based on a complete description of the species. The word 'description' means not merely taking note of their external form and organs—ie a sort of photograph—but also explaining them, so that valid comparisons may be made in order to discern the intricacies of their nature and identity. Nothing is really known until it is explained: it is not enough, for example, to note the occurrence of tendrils; it is also necessary to know whether the tendrils are foliar, cauline, or radicular (figs. 1 and 2), ie if they are modified forms of leaves, of axes—stems—or of roots. It is important to know if the organ of fixation of a plant is a true root or an axis, or if an inferior ovary² or a placenta is foliar or cauline, etc. The answers to such questions are very important for classification. The distinction between homology and analogy³ is therefore crucial; it is in fact the concern of comparative morphology, a science which is also fundamentally important for the systematist.

A complete description of a species, as we understand it, involves the co-operation of every scientific discipline; it necessitates a knowledge of the anatomical structure of

(1) This was the case with the *Prephanerogams*, which were confused with *Gymnosperms* up to 1942 because the ovules of these plants were taken for seeds.

(2) Inferior ovary: pistil situated below the petals and the sepals.

(3) Organs are said to be analogous if they are of different type but fulfil the same function, and homologous if they are of the same kind but have different functions (eg a leaf and a stamen).

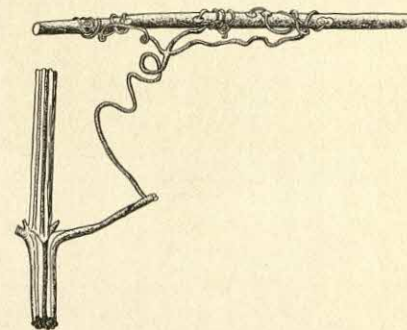


Fig. 1. Leaf tendril of *Pithecolitium phascoloides* Chm. (After Schenk).

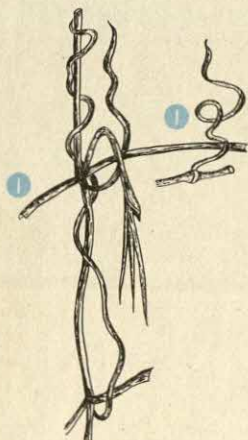


Fig. 2. Twining roots (1) forming tendrils, of *Zantrichia palustris*. (After Hochreutner).

plants, of their development (embryogenesis and organogenesis), their cytology and genetics, their chemical composition and serological properties, their physiology and ecology, and their reactions towards pathogenic agents, etc. Experimental methods are being increasingly used in the search for explanations; and every organism is studied historically, from the point of view of historical geography and genealogy. Here the collaboration of geology and palaeontology is essential.

Many of these disciplines, which are used to solve the problems of classification, are relatively recent. This means that our knowledge of plants is continually growing, new facts leading to new points of view, which may affect classification profoundly. This will always be true, so that classification is a creative and constantly progressing science.

The relative importance of characters

The question of the evaluation of characters is more delicate and subtle.

As the aim of classification is to group plants according to their natural, i.e. genealogical or phylogenetic, relations, we must consider their characters in relation to the genealogical order of their descent. There can be no question about this, for there are no more natural relationships between organisms than those of descent. Every effort must therefore be made to discover them, with the invaluable aid of palaeontology and the experimental sciences, for only these can provide infallible evidence of the hierarchy of the various characters.

In spite of the inherent defects of these disciplines, much has already been learnt from them. For example, the discovery of the palaeozoic Psilophytaceae⁴ threw much light on the origin of the vascular plants, and palaeontology furnished proof that the great groups of plants, Schizophytes,⁵ Algae and Fungi, Psilophytaceae, Vascular Cryptogams or Pteridophytes,⁶ Prephanerogams, and Phanerogams (Gymnosperms and Angiosperms) appeared in succession (fig. 7). This fact, together with the observation that each of these major groups has features in common with the one that preceded and the one that followed it, proves that they arose from each other in the chronological order indicated. It is clear, therefore, that in a linear scheme of classification we must put the Schizophytes at the bottom and the Phanerogams (Angiosperms) at the top.

In the course of phylogeny, not all the forms that existed at a given period gave rise to later stages. Some groups remained unaltered or evolved only within the limits of their own patterns. This explains why the world of today exhibits the great variety that we observe. This was not so, for example, in the Lower Devonian period: then there existed only Thallophytes (Schizophytes, Algae and the Fungi, deriving from these), Psilophytaceae and other Pteridophytes. Prephanerogams appeared in the Middle Devonian period and became important in the Carboniferous. Gymnosperms (conifers) are unknown before the Upper Carboniferous period, and reached the peak of their development in the Mesozoic. Finally, towards the end of the Secondary period, came the Angiosperms.

The terms 'higher' and 'lower' have been much abused in classification; they are not, in fact, very significant. All that matters is what is earlier or later, original or derivative, in the phylogenetic chain. We can say only that Angiosperms, for example, represent the most recent phylogenetic development, and that their pattern is much more complex than that of a unicellular alga; we often call them 'higher' because we are thinking of classification as a ladder on which they occupy the highest rung. But it is more correct to say that the features peculiar to Angiosperms are more recent than those of Gymnosperms, and that these are later than Prephanerogams, and so on.

Consequently, a character that is found in an ancient line and appears again in a younger line is an archaic one or a relic of one in the latter. This applies, for example, to a Gymnosperm character found in an Angiosperm. Conversely, an Angiosperm character seen in a Gymnosperm is a modern feature of evolution. Fig. 3 shows the ovule of a Pteridosperm (*Gnetopsis*), which is characterized by a skin with a thick *sclerotesta*. This feature survives unobtrusively in the ovule of a living conifer (*Callitris*), where it is an archaic character.

Thanks to palaeontology, we have some evidence of the directions in which phylogeny takes place, so that we can apply these facts, by comparison or generalization, to plants of which we have no fossils. In fact we can reasonably assume that phylogeny takes place in the same way today as it did long ago. However, although there seems to be a striking determinism in these phenomena, it is not as simple as we might wish. For example, it is taken as a rule that species with an inferior ovary are derived from those in which it is superior.

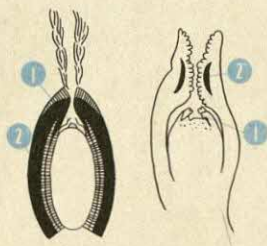


Fig. 3. Survival of an archaic character in a conifer ovule (*Callitris*). Left: ovule of a Pteridosperm of the Carboniferous period (*Gnetopsis*), whose covering, which is feathery at the top to catch pollen, has a thick layer of hard tissue (*sclerotesta*). Right: the covering is papillose and the *sclerotesta* has almost disappeared. (1) Pollen chamber; (2) *sclerotesta*.



Fig. 4. (Left): *Annularia longifolia*, hollow impression (below) and in relief (above).



Fig. 5. Fossilized fragment of stem of the plant *Calamites suckowi* Bgt.

Fig. 6. (Left): imprint of *Anotopteris distans* found in the neighbourhood of Stuttgart. (National Museum of Natural History, Paris. Photo Lod).

(4) Psilophytaceae: a very old group of vascular cryptogams, dating at least from the Silurian period.

(5) Schizophytes: the group linking the bacteria and the simplest algae (blue algae).

(6) Pteridophytes: synonym for 'vascular cryptogams' (see fig. 7).

This is doubtless often true, but it is probably not an invariable rule.

We know for example that in certain lines, types with inferior ovaries are earlier in time than those with superior ovaries, and also that some present-day species which normally have inferior ovaries can give rise to progeny including individuals with superior ovaries (*Epilobium*). If this feature persists and becomes the point of departure of a fresh line, it will be the beginning of a new type with superior ovaries. So the inferior ovary is not necessarily more recent.

These examples show that facts clearly established by palaeontology or observed inheritance, ie by history, should not be over-ridden, and that we must be careful what deductions we make from observations based only on living plants.

Primary and secondary characters

Some fundamental principles have now

been established in knowing that classification must be based on all the characters observed and evaluated in accordance with the criteria of history and genealogy, in order to define what should be called archaic or modern, old or new, lower or higher. We must now decide which characters should be given priority, or in other words which are of primary importance and which secondary or subordinate.

The greatest significance must surely be given to the reproductive organs, for the simple reason that they ensure the continuance of the species, and their gametes carry the physical basis of phylogeny, in the form of genes. The next most important are the vegetative organs.

This is a general guide; in detail the problem is presented in different ways according to the particular group under consideration. In the classification of a large group, in which the fundamental characteristics of the reproductive apparatus do not need to be considered because they are, naturally, the same in each member, great importance will be attached to details of the floral structure. Within a small group, for example in one species, the characters of even less consequence in the general plan, sometimes subtle ones, will take first place—such as the colour of flowers, the form of leaves, the presence and form of hairs, biological or nuclear features, and so on.

Multiple ancestry

It may well be that the privilege of breaking new ground phylogenetically is not reserved for one stock, but several. In other words, lineages marking a new stage of evolution do not have a *single* ancestor or a unique origin, but several; they are then described as polyphyletic or pluriphyletic. Conifers provide a striking example of this. These plants are derived from the Cordaites, but since their origin, in the Carboniferous period, conifers of the northern hemisphere have been different from those of the southern. This peculiarity has persisted ever since, and it is still very marked. Conifers are therefore certainly pluriphyletic. The same can be said of all the phyla, and also of smaller groups, such as orders, families, etc.

These considerations clearly show:

- (1) that if the primary groups of classification, the phyla or *divisions*, represent major stages of phylogeny, each of them includes not only directly related lines, but also a collection of

Fig. 7. Genealogical tree of the plant world.

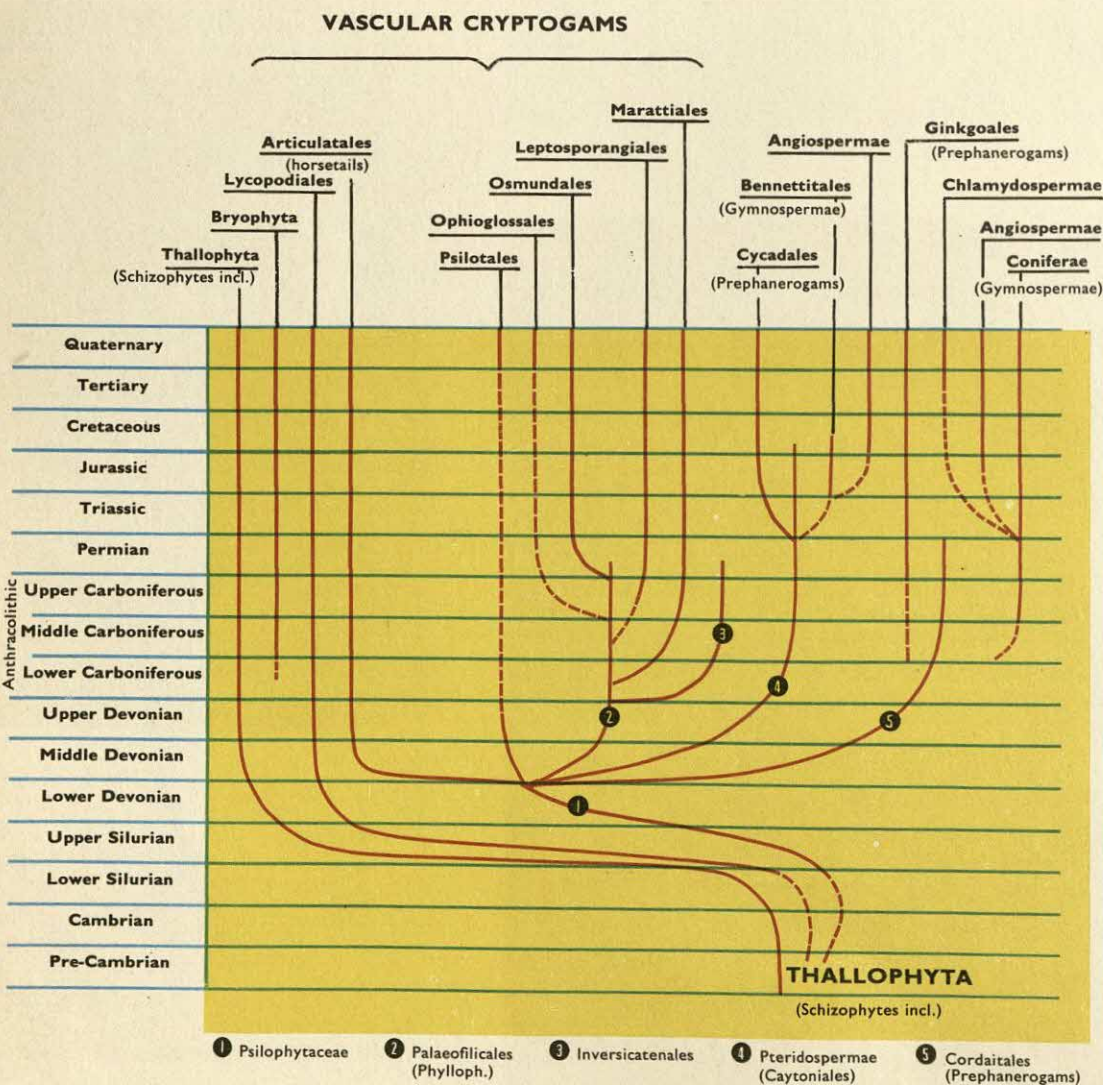


Fig. 8. *Cordaitea lingulatus* (Upper Carboniferous) from the mines of Commentry, France. (National Museum of Natural History, Paris. Photo Lod).

'cousins', each of which has its own place, but all at the same phylogenetic level, that is at the same stage of evolution;

- (2) that the concepts of primitive and modern, old and new, lower and higher, have no absolute meaning, so that their significance is limited to members of the *same line*, that is of the same ancestry. There are thus many ways of being 'higher' or 'lower'.

The future of classification

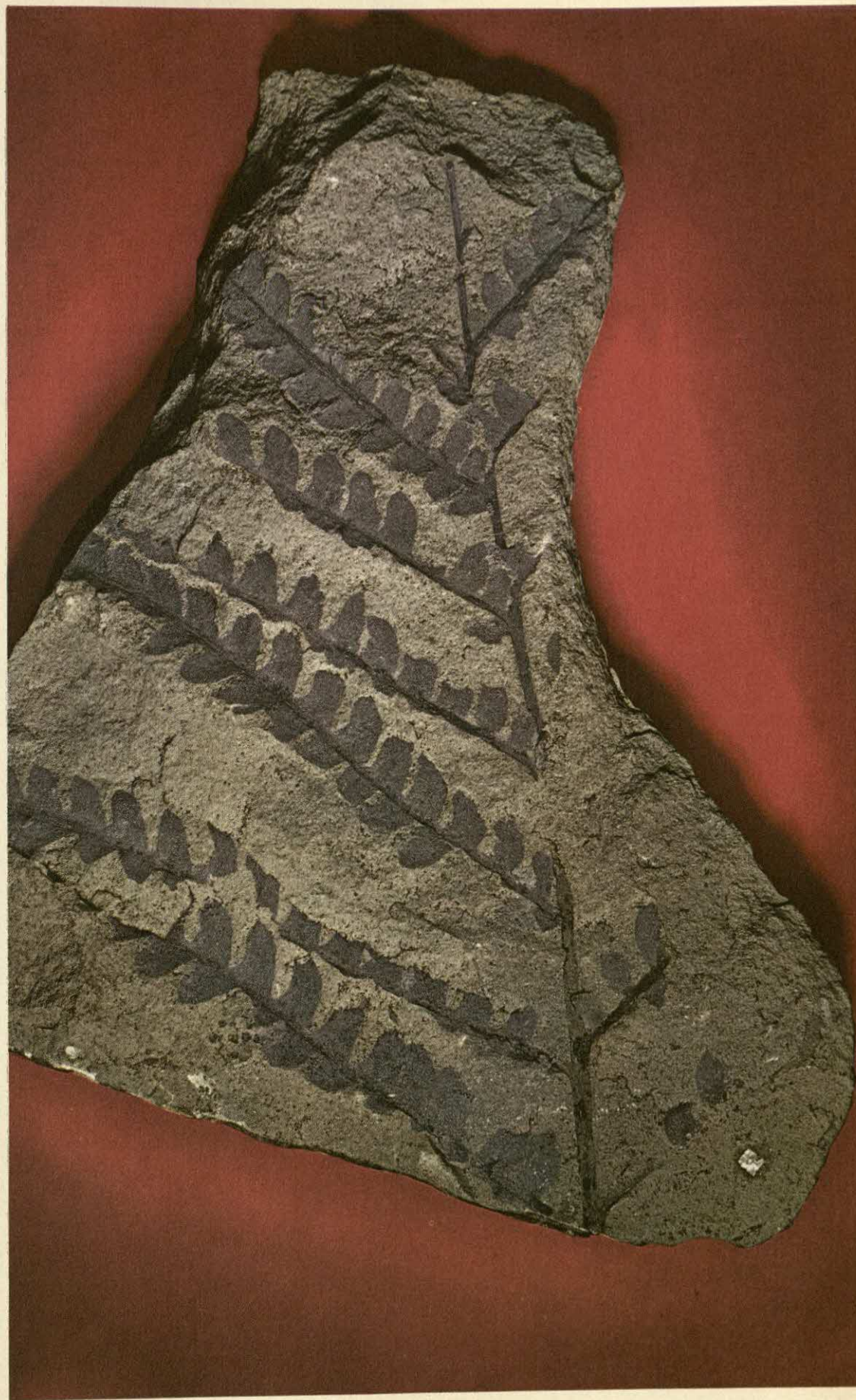
The ideal aim of classification would be to unravel the tangle of the world of today and to isolate each of its threads, ie to follow the descent of each line through all the stages of phylogeny, right back to its origin.

Great progress has already been made in this direction, but the achievements are small compared with what still remains unknown. We are already in a position to abolish long-accepted groups of classification, such as Gamopetalae and Monocotyledons, since we now know that the plants grouped in these categories represent the latest phylogenetic stage reached by certain lines.

The Rubiales, for example, are the 'gamopetalous' stage of a line that includes, among others: the Terebinthaceae and Umbelliferae on an equal footing; the Primulas and the Plumbaginaceae—formerly considered as inferior Gamopetalae—belong to the group of lines that also includes the Urticaceae, Polygonaceae, Centrospermae, etc; the Spadiciflorae belong to the same strain as the Piperaceae; Helobiae and Liliales incline towards the Polycarpa, etc.

Fig. 7 shows the main branches of the genealogical tree in the present state of our knowledge.

But we are far from the final objective, which would be a complete genealogy of the plant world, similar to that of human families, but much more difficult to establish. Its achievement will be limited by human failings, and will depend on the parallel development of all the disciplines whose discoveries are used as fast as they are made. It must model itself constantly on these discoveries, and be adaptable and always prepared for reconsideration: a magnificent effort, one worthy of the utmost of human ability.



Flowerless plants

Henri J. MARESQUELLE

(1) This pattern is seen also in colonial Flagellates; these grow in groups of a definite number (16 in *Pandorina*, 32 in *Eudorina*, and 500 to 20,000 in the various species of *Volvox*) on the surface of a gelatinous sphere that floats in fresh water, and they make the colony move with their cilia (fig. 4). Owing to the fixed number of elements, the only function performed by mitosis is to build up the colony. But encystment, reproduction and sexuality do take place: in *Eudorina*, each flagellate in the sphere may form a cyst, and after a resting period may divide into a number of individuals, which build up a new colony together. If gametes leave the colony and form fertilized egg-cells, encystment and reproduction still occur.

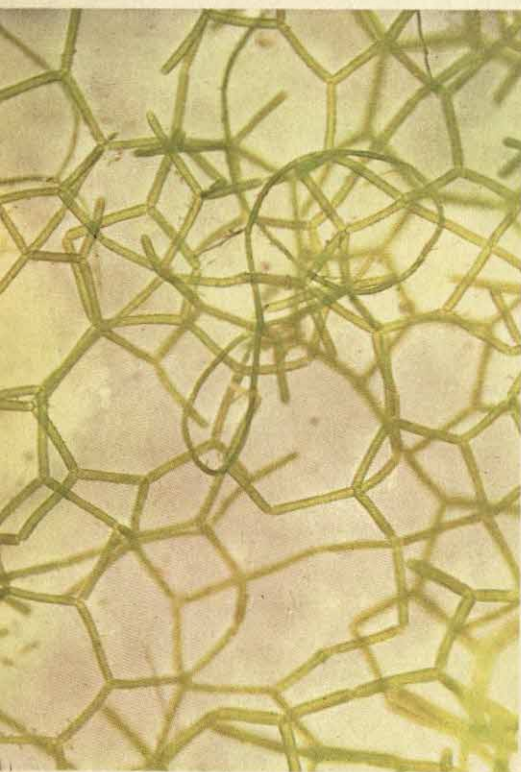


Fig. 1. Fragment of the three-dimensional network formed by the freshwater alga *Hydrodictyon reticulatum*. (Lod).

Can we speak of 'flowerless plants'? Does not this negative term imply that a variety of disparate organisms are being included together in one group? To present flowerless plants as a radiating group of lines arising from the Flagellates makes them appear as a collection of independent series, with parallel life-stories, but without any obvious link in origin. We shall see, however, that flowerless plants cannot be described without at the same time considering the basis of all life.

The basic problem concerns the life cycle. This expression denotes a cyclical series of well-defined biological activities, among which we may distinguish: a vegetative phase of growth and vigorous metabolism; a reproductive phase, leading to fragmentation and dispersal of germ cells; a resting phase, in which there is maximum resistance to unfavourable environment; and a sexual phase, which may possibly coincide with one of the others.

The lowest forms of plant life (Pseudocaryotes, ie bacteria and algae), exhibit these phases, but grouped in a way which we rarely see elsewhere. The vegetative and reproductive phases are ill-defined and there is constant cell division. As the cells of bacteria or blue algae are arranged in clusters, chains, or other kinds of groups held together by mucilage, it is doubtless possible to distinguish the growing phase that produces such groups from the reproductive phase that initiates new ones; but this distinction is neither regular nor general. The resting phase is very important in most of the blue algae, and in the so-called spore-bearing bacteria. A spore is formed by contraction of the protoplasm within the membrane, and the spores that result can survive extreme conditions. When sterilizing water, for example, it is necessary to raise the temperature above 120°C to kill bacteria in the form of spores. Lastly, the sexual phase occurs very irregularly: it is unknown among the blue algae, but has been discovered and

studied in certain bacteria. But although sexuality exists in bacteria, there is no sign of sexual reproduction. When an individual transmits a character to a partner, this does not result in an additional individual, so there is no reproduction as such, but there is production of a new hereditary type, ie a new strain.

Among Flagellates, the lowest group of the Eucaryotes, the situation is analogous to the one which has just been described in Pseudocaryotes: no clear distinction between growth and reproduction, entry into a resting phase in the form of a cyst, and very unevenly distributed sexuality, without reproductive significance, whose only function is to renew the race by cross-breeding (fig. 4).

One group of Flagellates, the green ones, deserves special mention, because it is the ancestor of all green plants and also because it displays more pronounced sexuality than other groups. The free-swimming forms, such as *Chlamydomonas*, for example, reproduce by cellular division. The process of mitosis, which is in all higher organisms a growth-mechanism, is here devoted to reproduction. However, even at this level, we may see the beginnings of a more authentic reproductive process from which is derived, in the higher plant world, the whole system of reproduction by spores. This phenomenon is associated with the resting phase: the flagellate that leads its active life swimming in the water, becomes an encysted

immobile cell, without flagella, encased in cellulose. Now the cyst germinates only after undergoing two or three series of conjugated mitoses (synchronous) inside its membrane: it will then contain first two, then four, and often eight little cells, which acquire flagella and escape by rupturing the cyst wall. A phase of cellular growth follows, then some ordinary mitoses, then further cyst formation, which indicates both rest and multiplication. In the fairly frequent cases when these green flagellates copulate (by the union of two individuals and the fusion of their nuclei), the resulting fertilized egg-cell becomes a cyst and returns to active life only after undergoing conjugated mitoses. Here we have a connection between sexuality, the resting phase and reproduction. For all these organisms this type of reproduction is non-obligatory: they can multiply either asexually, by a reproductive cyst arising from an ordinary flagellate, or sexually, by a reproductive cyst originating from a fertilized egg-cell.¹

In all these organisms there is the problem of the cytology of the life cycle. The cell contains a complete nucleus; two nuclei (male and female) join together at the time of copulation; a double (diploid) nucleus is thus formed, and there is also a compensatory process, which normally restores the nucleus to the simple (haploid) state; this reduction (meiosis), which restores the simple number of the chromosomes occurs during the germination of the egg-cyst. It was observed many years ago in the case of *Volvox* that only the fertilized egg-cell has 24 chromosomes, and that its first divisions reduce the number to 12, which is characteristic of the rest of the cycle.

Alga, moss and fern cycles

This type of meiosis following immediately upon fertilization is termed 'zygomeiosis', and is very widespread among lower plants. It helps to define an important part of the life cycle of green algae, some features of which are shown in fig. 5. There are alternative kinds of reproduction, one sexual and the other asexual, both associated with intense mitotic activity inside a cyst, and both producing the same type of cell because zygomeiosis cancels the effect of doubling the number of chromosomes. The essence of sexuality is still the renewal of the race by the mixture of different hereditary strains; but the associated reproductive process consists in proliferation of the egg-cell and the production of large numbers of sexual germ cells or gametes.

In several groups of green algae the cycle

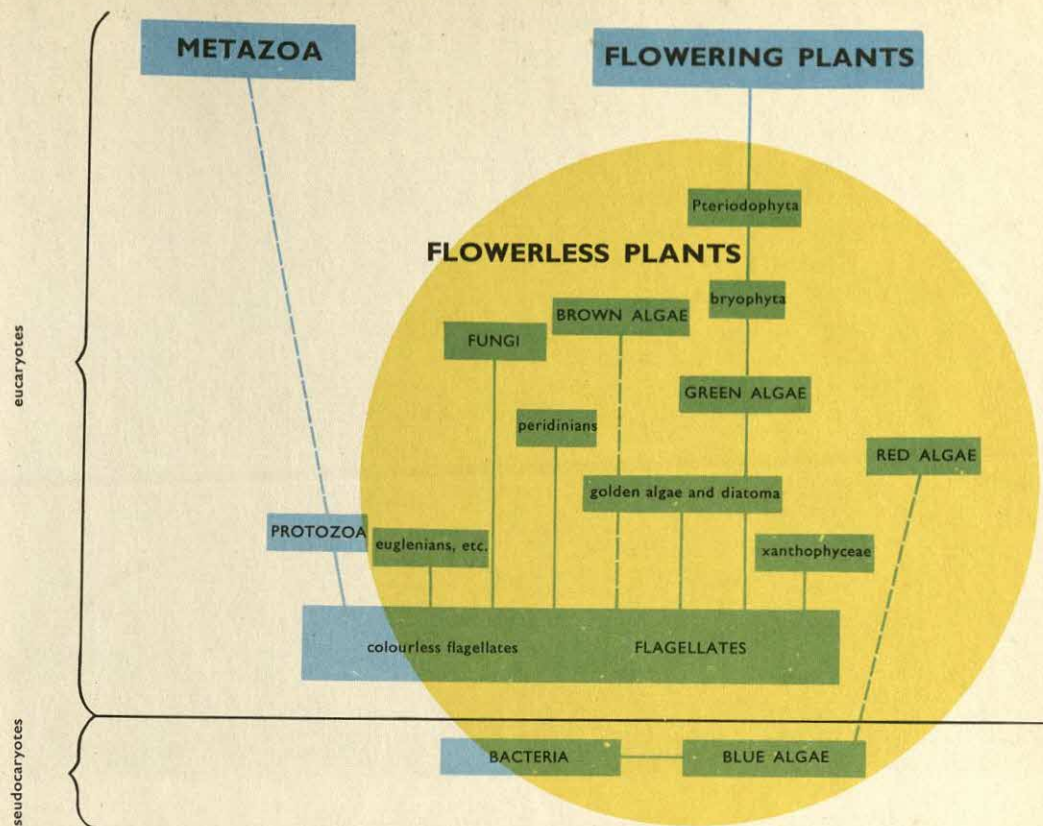


Fig. 2. Diagram showing the position of flowerless plants in the vegetable kingdom.

is different. Meiosis does not occur immediately after fertilization, but is delayed, and so there is a diploid phase. In the Ulvaceae, fresh green laminae which grow on the sea-shore, the cycle consists of phase alternation. There are apparently two plants, the haploid which produces gametes and is therefore called the gametophyte, and the diploid which grows from a fertilized egg-cell and produces spores (whence the name sporophyte) by a process of meiosis in a cyst, which is henceforth known as a sporangium. Thus the two types of reproduction, which can replace each other, are linked together in a true cycle² in this case.

The Bryophyta (mosses and liverworts), and Pteridophyta (ferns, etc), whose anatomical and histological structure is far superior to that of most algae, have certain chemical characteristics which resemble those of green algae. These characteristics are all the same, for they have the same assimilatory pigments (the two chlorophylls and carotinoids³), and the same end-product of assimilation (starch). Since these features are very constant in green algae and Flagellates, they provide good evidence that their ancestry is the same. But what is the relationship between green algae, Bryophyta and Pteridophyta as regards the life cycle? In this case it is always of the type known as the alternation of generations.

(2) In the great group of Siphonales, meiosis is carried even further back; it takes place during gametogenesis, as in animals, so that the diploid state persists throughout their life. In its essentials, the situation is similar in other groups of algae, particularly the brown. These culminate in the most highly evolved groups of Laminariales and Fucales. An additional characteristic of the former is their great size, both on our shores and in the northern seas, where the giant *Macrocystis* types, up to 300 metres long, occur. These highest groups have cycles similar to those described above, i.e. alternation in the former, and persistence of the diploid state in the latter. Thus, here also, evolution results in delayed meiosis and obligatory sexuality.

(3) Carotinoid: a coloured pigment very commonly found in plants.

(4) Ascus: the mother cell in which the spores of fungi are formed (see M. Chadeaud, 'The Abundance of Plant forms').



Fig. 3. This moss colony (*Funaria hygrometrica*) contains two kinds of generation: haploid (the lower, leaf-bearing part), and diploid (the upright organs called 'sporogonia'). When young, the sporogonium has the form of a spear which later differentiates into a peduncle and a swollen tip, the urn, which contains the spores. (Photo Lod).

(5) Mycelium: vegetative part of fungi.

(6) Somatogamy: the union of two vegetative (non-reproductive) cells of the plant-body or 'soma'.

(7) Gametangium: the organ that produces the gametes.

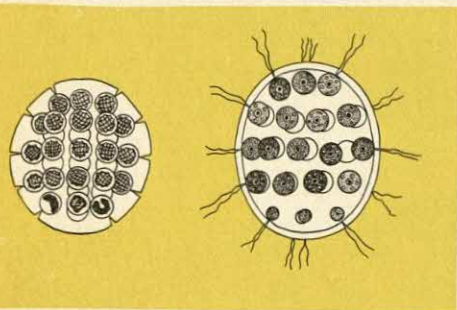


Fig. 4. Reproduction in Flagellates; the pattern in Eudorina. Left: a colony of flagellates. Right: each flagellate has divided and a cyst has been formed.

Mosses, for example, consist of a small leaf-bearing plant with sexual organs; as a result of fertilization a leafless stem develops from the female organ, and its cells are diploid; this stem bears a capsule in which reduction of chromosomes occurs and haploid spores are liberated. Sexual reproduction is thus an integral part of the cycle, alternating with sporulation (fig. 3).

Ferns have the same life cycle, but the diploid part, attached to the haploid to begin with, becomes a plant of considerable size, i.e. the fern; the haploid is a little green lamina bearing the sexual organs.

All these plants, Bryophyta and Pteridophyta, show progressive adaptation to life on dry land. Most mosses still stand in water, with only the capsule in the air; ferns need water only during the haploid phase of sexual reproduction.

This has two consequences:

(1) The resting phase assumes a greater importance than in the less exposed aquatic plants, and it occurs at a point in the cycle that is not the same as in the lower algae; it is the spores resulting from meiosis which envelop themselves in a protective membrane. Their protoplasm dries up and they are scattered by the wind, and the plant is preserved through a long period of drought. This timing of the

resting phase is characteristic of all Bryophyta and Pteridophyta; the change which will take place afterwards, replacing the resting phase by the seed stage (the stage of the young embryo surrounded by food-reserves) will provide a definition for a new group, that of plants with seeds, which includes all flowering plants.

(2) Pteridophyta show that the haploid element is becoming smaller and smaller. In a selaginella it is scarcely bigger than the spore from which it grows, which points the way towards flowering plants in which the haploid element is only a short-lived tissue in the heart of the flower. The same sequence occurs, by a gradual process of evolution, as in green algae (leading to the Siphonales), in brown algae (leading to Fuciales), and in the whole of the animal kingdom; in all these cases, evolution results in individuals of large size and perfected structure, composed of diploid cells that give rise, more or less directly, to haploid gametes; and these are formed regularly, since sexual reproduction has become an essential part of the life cycle.

The sexual evolution of fungi

Fungi are quite different from green plants; moreover, their origins seem entirely different. Nevertheless there is a biological similarity between these two great groups: both leave water and take to the air and dry land. This phenomenon, which, as we have already seen, was important for green plants, plays an equally great part in the life of fungi.

An extreme example of the Basidiomycetes is the *Fomes*, a giant Polypore which lives parasitically on tree-trunks, where it forms large tough masses: by its great size, long life (of which the annual growth-lines are evidence), and the unusual composition of its tissues, both hard and resistant to decay, this plant shows traces of a very advanced evolution. Now, it is one of the most aerial fungi.

Among the Ascomycetes, some little coprophilic species (i.e. living on animal excrement), such as *Bombardia*, *Sporormia* and the *Ascoboli*, are notable. Their greatest refinement is not their size, but their mechanisms of dispersion; their spores are scattered by what one might call a ballistic method. The ascus⁴ containing them behaves like the cartridge in a revolver: each ascus moves forward in turn, activated by a mechanism (not yet fully understood) which swells its membrane or vacuole; on reaching the firing position it explodes and shoots the sticky packet of spores some distance away (fig. 6). The spores may

adhere to insects which scatter them about, but more often they fall on grass, and are spread farther afield through the digestive tract of herbivorous animals. This form of dispersal, by animal means, is a good example of adaptation to a terrestrial environment.

Then we have, in contrast, an example of a lower fungus, which is still aquatic and closely related to the Flagellates, *Entophlyctis*, which keeps its flagellum only for a short time. It turns into a kind of giant amoeba, with extraordinarily branched pseudopodia, which attacks certain water plants (fig. 9); this sort of pseudopodium is like the mycelium⁵ of a fungus, and there are in fact several species showing a gradual transition between this and the true fungi.

The sexual reproduction of fungi is very complicated, but the following facts about it are of interest.

In the Basidiomycetes, which are considered to be the highest form of fungi, there is no longer any sign of the type of reproductive organs seen in all the lower groups. These organs, which consist of the swollen extremities of filaments, and often show curious types of sexual tropism, have completely disappeared in the Basidiomycetes, where fertilization occurs by the union of ordinary filaments (or somatic elements, whence the term somatogamy⁶). The most extreme form of somatogamy is the diffuse fertilization seen in many higher fungi (eg coprins), and particularly parasitic ones (such as the rust fungi of cereals). A virgin mycelium grows and spreads its area and thus comes in contact with a mycelium of opposite sex. The two mycelia immediately join together, and nuclei from each invade the other's filaments: soon afterwards (perhaps in a few hours) complete cross-fertilization has occurred (fig. 8). This is the only example in the living world where sex consists of two organisms coming together, uniting and fertilizing each other throughout their whole extent, down to their very cells.

If it is true that fungi tend to abandon previous forms of sexuality, as we have just seen, new organs, sometimes of bizarre type, repeatedly appear in this group to promote sexual reproduction. They use aerial methods, either the wind or insects, to promote copulation. *Neurospora*, humble wood-moulds that sometimes spread to bakeries and have been used in the laboratory for the study of genetics for the last thirty years, have very fine light spores, which are scattered by the slightest breath of wind. These asexual elements, called conidia, are of two kinds: the

large ones (macroconidia) distribute the species very effectively, while the small ones (microconidia), with minute cells and hardly any protoplasm, cannot produce a vigorous mycelium but are able to transfer their nucleus (which is the normal size) to a colony of the opposite sex.

The same thing is seen in many other fungi, eg the coprins, where a special kind of spore, called oidia, occurs in several forms; some of them are very small, and although they lack effective reproductive power they can fertilize others. In contrast with the previous example (anemophily), this is entomophily: the oidia are formed in drops of liquid and gathered by insects.

There are other more advanced examples. Some Ascomycetes such as *Bombardia*, and Basidiomycetes like the Uredinales, develop in special organs minute spores (spermatia), which are carried by insects, thus permitting the species to fertilize over great distances. In the case of the Uredinales the insects are attracted by bright colours, the secretion of nectar (pear-tree and barberry rusts) or sometimes by scents (spurge and thistle rusts).

The fungi have not only changed their

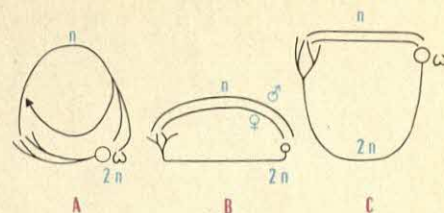


Fig. 5. Three life cycles in algae: (A) purely haploid (zygomeiosis); (B) alternation of generations (meiosis); (C) purely diploid.

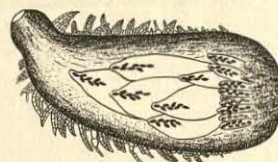


Fig. 6. Peritheca of *Sporormia*, containing at the right some young asci (with their spores); above, the asci are distended, rising to the firing position; on the left is the muzzle of the fire-arm, from which the spores will be ejected.

Fig. 7. Formation of the organs of fructification in a coprin. (Photo Lod).



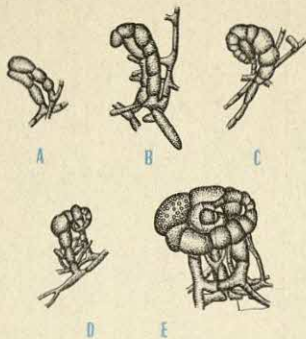


Fig. 8. *Ascobolus magnificus*: the female gametangium gradually entwines the male one.

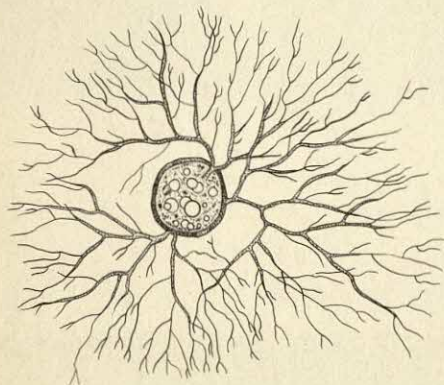


Fig. 9. *Entophlyctis*.

reproductive pattern by adapting themselves to aerial methods; they have likewise caused a reconsideration of the fundamental ideas of the nature of sexuality. In many of the higher Basidiomycetes (especially the coprins) and in the parasitic Basidiomycetes (Ustilaginales) there may be more than two sexes. Two phenomena may be observed, either separately or both together: geographical multi-sexuality (so-called because it varies according to locality) and sexual quadripolarity. Let us consider the second.

If the production of spores by a particular strain (eg a coprin) is analyzed, four sexes instead of two are found in many species. These four types have sexual affinity in pairs only: it is found that one sex (A) will unite with only one other (B), and the third (C) only with the fourth (D). In these species there are therefore two kinds of family: one that has an A and a B for parents, and the other that has C and D; but these two kinds of family resemble each other in that both of them have 'children' of the four types in more or less equal numbers; but when they grow older and become sexually active themselves, the young As are attracted only to the Bs, and the Cs to the Ds. Thus the two types of union are repeated, and children of the four sexes will again be produced. This strange sexual pattern can be readily explained in terms of heredity. It is only necessary to postulate that the sexual affinity between partners is determined by a double difference, carried by two independent genes. But it is a remarkable fact that these higher fungi are the only living organisms to depart from the classical pattern of two sexes.

To crown this remarkable pattern of sexual behaviour, the fungi often suddenly abandon sexual union: there are many examples where the sexual function in a particular race or species is degraded, especially among the higher fungi. Just as in higher plants (such as some Compositae, the dandelion, certain Rosaceae, etc), and in some insects such as the weevil, certain species are observed to reproduce themselves parthenogenetically instead of sexually, so there are many examples of fungi in which one of the sexes acquires the power to develop by itself, without fertilization being necessary. Cases of true parthenogenesis are in fact rather rare; but we must mention a mechanism that is very widespread among fungi, ie 'adelphogamy'. This term means the 'marriage of brothers', and it is applied to the union of two nuclei of the same origin, often two brother nuclei (ie

those resulting from the same mitosis), so as to effect nuclear fusion and make useless the union with a strange nucleus. The interlocking of two gametangia⁷ of *Ascobolus magnificus* has been observed; in *Ascobolus citrinus*, if the female gametangium does not meet a male and so has no opportunity to interlock, it remains unfolded; but it is fertile all the same and fructifies, bearing spores. In order to do this, two of its nuclei unite; these are of course two female nuclei of the same origin (and therefore sisters or cousins). Similar processes, in which the female (or indeed one of the sexes in somatogamous species, where the word female has no meaning) is enabled to be fulfilled through the union of two of its own nuclei, are found in all groups of Ascomycetes and Basidiomycetes. This phenomenon resembles parthenogenesis, in that cross-fertilization is eliminated and the race is carried on by a single strain, but differs because there is still the sexual 'ceremony' of the union of two identical nuclei. This contributes nothing new to heredity, and is a functionally degraded form of sexuality that has lost its significance.

What conclusions can we draw from this amazing story of the sexual cycle of fungi? On the one hand, these organisms abolish the old sexual pattern, but, while thus tending in the direction of somatogamy, they originate completely new structures which, though not themselves sexualized, nevertheless have an important influence on sexual function. On the other hand, having improved, diversified, and completely altered sexuality, they very often give it up altogether. This story seems at first to be full of contradictions.

However, there is another way of looking at it.

Sexuality is a kind of mechanism for ensuring the evolution of species. It is to be expected that the fungi should perfect their sexuality, and adapt it closely to a new way of life. But successful evolution does not necessarily imply constant change; when a favourable variation occurs, it is associated with a phase of stability. It is therefore quite natural for change to cease at certain times in this or that living creature, and for sexuality to be abandoned. This phenomenon in fact occurs in several large plant, and also animal, groups.

What is so remarkable in the fungi is that the two evolutionary processes of development and abandonment are seen side by side in them. Fungi are the only group in the whole living world where the two opposite methods, of sexual and asexual reproduction, are used with such eclecticism.

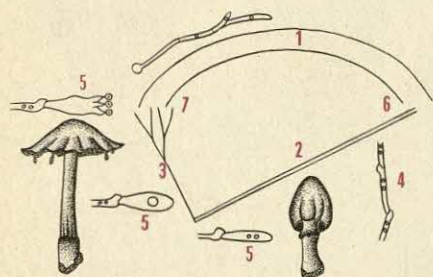


Fig. 10. The cycle of a coprin: (1) uninuclear cells; (2) binuclear cells; (3) diploid cells; (4) dicaryon; (5) basidium; (6) copulation; (7) meiosis.

Flowering Plants

René NOZERAN

Everyone, from his earliest childhood, learns to recognize flowering plants. Their names alone conjure up a vision of enchanting colours, principally white, blue, violet, red, pink, and yellow, set off by the green of leaves; delightful scents, sweet, strong, fresh or fiery; and the satisfaction of a harmonious pattern whose constituents are the 'golden numbers', balanced, orderly, or fantastic in shape. However, these riches normally belong only to the sterile parts of the plant, and the true characteristics of flowering plants, the reproductive organs that ensure the continuance of their life cycle, are hidden.

Although their subject may have changed with the advance of knowledge, discussions on the life cycle of flowering plants, while no longer controversial, are by no means exhausted.

For a long time, opinions held on certain points were diametrically opposed. Thus, from ancient times, following the lead of Pliny, up to the end of the eighteenth century, some recognized the existence of sexuality in plants; while others, convinced by the teaching of Aristotle, considered it to be exclusively restricted to the animal kingdom, in spite of cogent evidence to the contrary. To the latter, the application to plants of the adjectives male and female merely indicated differential characters, and in no way implied the idea of sexuality.

Cesalpino, the great botanist of the sixteenth century, considered that the better development and greater fertility of female date-palms, observed when they grew near the male palms, resulted simply from a kind of exhalation from the male, 'which re-warms the feeble heat of the female, so enabling it to bear fruit' (Guyénot, *Science and Life in the Seventeenth and Eighteenth Centuries*). Even Malpighi, the pioneer of plant histology, between 1671 and 1686 described stamens and pollen grains, studied the embryo and embryo-sac, and followed the development of the seed, without realizing that all these structures are a part of the mechanism of sexual reproduction.

It was only in 1877, less than a hundred years ago, that Strassburger observed for the first time the fusion of male and female nuclei

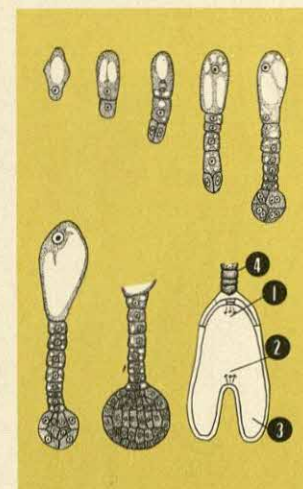


Fig. 1. Some stages in the embryonic development of *Capsella bursa-pastoris*. The first stage corresponds to the egg, and the others to the pro-embryo, except the last, which depicts an embryo with: (1) root meristems; (2) shoot meristems; (3) the rudiments of the two cotyledons. The cellular stalk supporting the pro-embryo and the embryo is the suspensor (4). (After R. Souèges).



Fig. 2. The castor-oil seed, intact (left) and in section (right) showing the embryo surrounded by the albumen.

(1) Meristems: groups of cells that have retained embryonic characteristics, ie they have undergone little or no differentiation.

(2) Leaf primordium: presumptive rudiment of a leaf.

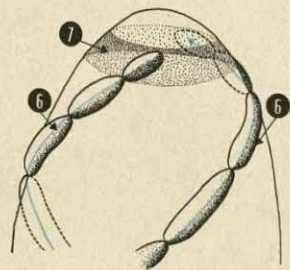


Fig. 3. Diagram of the tip of a stem with two leaf spirals (6) whose generative centres are situated in the initial ring (7). (After Plantefol and Buvat).

and so took the great step forward to recognizing the act of fertilization in plants, once and for all putting an end to the purely scholastic arguments that had been going on for a very long time.

Since then, much work has been done to establish the facts of plant life, opening up new horizons and raising fresh problems. In the following pages an attempt is made to outline some of these phenomena.

Germination of the seed

The most striking and universal feature of the seed of plants is its state of suspended animation. By the time a seed is ripe it has lost nearly all its water, and its exchanges with the outside world are reduced to a minimum. Of course, so long as the seed is alive, respiration goes on, but only very slowly; and all the accompanying physico-chemical processes are also reduced to a minimum.

The seeds of many plants can germinate only when certain external conditions are fulfilled; until then they are said to be dormant. This state of dormancy is more striking in some species than in others. We now know that dormancy may be due to several causes. For example, the impermeable coverings of seeds may be responsible for keeping the seed dormant, by preventing the access of water and oxygen to the embryo (many Leguminosae, and certain aquatic plants). In these cases, the seed cannot germinate until its covering has been ruptured and water can get in. Elsewhere, germination may be inhibited by chemical substances present, for example,

in the covering (*Pectis papposa*, Went) or even in the pulp of the fruit surrounding the seed (tomato, pear, apple, lemon). Lastly, there are seeds (eg the mountain ash, *Sorbus aucuparia*) whose internal tissues control dormancy. In this case dormancy can be terminated only by certain internal changes, which are mostly caused by cold (stratification), dehydration, light, or chemical agents (gibberellins).

Growth

The purpose of the meristems¹ of the hypocotyl (young stems) and the radicle, which to begin with are nourished by the seed's accumulated reserves, is accomplished in the formation of a tiny plant, equipped with a root and leaves, and capable of leading an independent and autotrophic life from then on, provided it is in suitable surroundings. In the course of growth the root of the young plant will grow and branch out, and new leaves will grow from the stem. As a general rule, in the axils between the leaves and the stem, buds are formed from which secondary branches grow.

Although variable, the structure of the terminal meristem of the stem can usually be described in terms of the general diagram offered by Buvat. Two essential regions can be distinguished: a central one which



Fig. 4. Boughs of *Allierandia procera* from Madagascar. The leaf spirals are easily seen. (Photo Decoins).

constitutes the dormant meristem and shows few cell divisions; and a peripheral one, the initial ring, where the mitotic activity is intense, and where new leaves make their appearance.

These last do not appear in a random order. The study of phyllotaxis, ie the arrangement of leaves on the axis of the stem, has advanced considerably, mainly through the work of Plantefol and of Snow, who have established that leaves start along a number (occasionally only one) of spirals, each of which arises from a 'generative centre' in the initial ring. Loiseau furnished the experimental evidence for these centres. In *Impatiens Roylei* Walp, for example, he damaged part of the initial ring, and provisionally altered the pattern of phyllotaxis by reducing the leaf spirals of a stem from three to two (figs. 3 and 4).

What is the part played by the dormant meristem in these processes? According to Buvat, its role in the construction of the vegetative part of the plant is negligible. In fact, however, the meristem seems to have the dual function of building and organizing. The former is suggested by comparison with algae or vascular Cryptogams: the infrequency of cell divisions resembles the 'mitotic inertia' in the apical cells of certain algae (*Chara*, for example) or vascular Cryptogams (ferns), in which the active division of the daughter cells of the apical ones eventually results in the construction of the plant. The work of Steeves, Sussex, Cutter and Wardlaw suggests the organizing function. They have shown that isolation of the apical meristem of a very young leaf primordium² determines its growth into an axially symmetrical organ, like the bud of a branch. It seems, therefore, that certain cells of the growing point,³ which may be situated in the dormant meristem, control the development of the stem.

Both external and internal factors can also have their effects, as is the case with the process of embryonic development.

External factors, such as shorter days, can start off a series of internal processes which may lead to the function of the apical meristems being suspended, and dormant buds being formed. In some ways this is similar to what happens with seeds, whose growth can be awakened by certain physical factors (eg cold) or chemical agents (ether, chloroform, acetone, gibberellins, etc).

There are also some factors which are specifically internal. The terminal bud and leaves, for instance, often produce auxins,

substances that inhibit the development of the lower buds of the plant. This inhibition may be relieved by simply cutting off the terminal bud. In the same way, other internal factors appear to control certain differentiations and their existence at the level of the meristems is revealed by a curious and unexplained fact. Some plants produce several types of branch without the influence of any external factors; they appear with strict regularity at fixed points, and the transformations, once begun, are completely irreversible. Plants belonging to different families, *Cephalotaxus* (Gymnosperms), coffee-tree (Rubiaceae), *Paliurus* (Rhamnaceae), *Phyllanthus* (Euphorbiaceae), etc, have orthotropic and plagiotropic branches. They are distinguished by their shape, as the symmetry of the former is usually radial and of the latter bilateral; as well as by their geotropism⁴ (negative for the first and intermediate in the second). The persistence of plagiotropism,⁵ although secondary to and derived from orthotropism,⁶ is sometimes astonishing; in the coffee-tree, for example, and in certain Gymnosperms, a cutting of a plagiotropic branch gives rise to a plant which has no orthotropic properties.

Fig. 6. The little green prominence at the centre is the shoot meristem (growing point) of *Lupinus albus*. The whole stem, with its leaves and lateral buds, will arise from this. The most recent leaf rudiments can be seen just below the meristem. Older leaves have been cut away, because they are normally folded over the meristem. (Photo Lod).

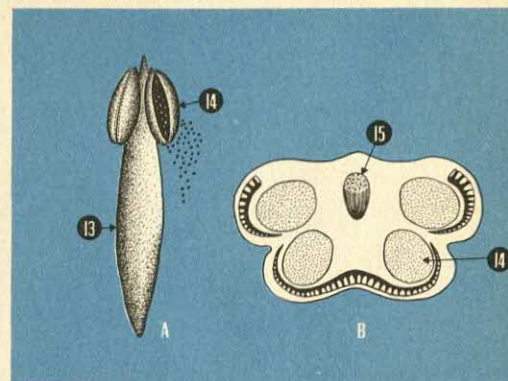


Fig. 5. A. diagram of a stamen: (13: filament; 14: pollen sacs). B. section across pollen sacs: (15: vascular bundle).

(3) Growing point: the apex or tip of a stem or a root.

(4) Geotropism: the influence of gravity on the growth of a plant.

(5) Plagiotropic: this describes a structure that grows horizontally under the influence of gravity.





Fig. 7. The anther of a pink, liberating its pollen grains. (Photo Lod).

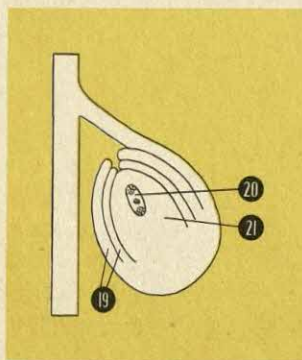


Fig. 8. Cross-section of an ovule: (19: integuments; 21: nucellus; 20: embryo-sac).

Perhaps observations made on micro-organisms will help us to interpret these phenomena. The development of plagiotropism might be regarded as the result of a modification, which had been induced at certain points, in the function of the cellular genotype. In the cytoplasm such a modification would lead to new or at least transformed self-reproducing elements being formed, which would be more directly responsible for the change.

The reproductive phase, or more precisely the period of sexual activity, begins with the preliminary transformation of some of the vegetative buds into flowers. The factors determining this change vary in different plants.

Reproductive organs

Some species flower when they reach a particular stage of vegetative growth, called by Klebs 'floral maturity'. This stage is independent of external factors, so long as these do not interfere with the plant's nutrition (chickweed: *Stellaria media*, *Senecio vulgaris*, *Poa annua*: see fig. 12).

By contrast, other plants need external stimuli to make them flower. For example, some require a period of cold (winter wheat), others a particular night and day (nycthemeral⁷) rhythm, with either short days (some chrysanthemums, tobaccos, etc) or short nights (spinach, scarlet pimpernel: *Anagallis arvensis*, *Calluna*, etc). Yet others require a suitable combination of the two factors (henbane: *Hyoscyamus niger*).

The internal changes which these external factors initiate are still unknown, but in certain species the graft of part of a 'ripe' plant conveys this property to an untouched piece of stock. It should also be mentioned that flowering can sometimes be induced by chemical agents (vitamin E, gibberellins, dihydrofolliculin, acetylene, etc).

Whatever the factors determining this phenomenon, the result is that the terminal meristem of the stem acquires a new function. In contrast with what occurs during the vegetative period, the cells of the dormant meristem start multiplying to form rudiments of most of the floral organs; only the most external parts are still produced by the initial ring.

The flower

The significance of this development is still unknown, but the end-result of it is always a flower.

Its general pattern is a group of asexual parts, the perianth, whose sepals and petals constitute the calyx and corolla respectively. The sexual parts consist of a male portion, or androecium, formed by the stamens, and a female portion, or gynoecium, represented by the carpels. There has been much argument about the nature of these various parts, but evidence obtained from the comparative anatomy of living and fossil forms, and from normal and deformed plants, seems to confirm what Goethe thought, that is that they were modified leaves, though this interpretation is rejected by some modern authorities.

Recent studies by Emberger, Lam and others have also established resemblances between various floral organs and the vegetative and reproductive apparatus of both fossil and living vascular Cryptogams.

There are many variations on this basic pattern, covering the arrangement and form of the different types of organ, and also their number, which may be reduced to zero. For example, there are flowers without androecium or without gynoecium, which are therefore unisexual, either male or female.

The reproductive organs themselves, which we shall consider only in the Angiosperms, are, as we have seen, the androecium and gynoecium. The stamens of the former consist of a sterile part, the filament, which bears the anther containing four pouches joined together, in which the pollen is formed: these are the pollen sacs. Similarly, the gynoecium consists of sterile portions, the carpels proper, and the ovules. The latter comprise, enclosed in one or two integuments, a central mass or nucellus, which itself contains the embryo-sac (figs. 5, 7, 8, 10).

The important moment in the development of these elements is before the formation of the pollen grains and embryo-sac. The cells that will give rise to them undergo chromatic reduction (meiosis), ie the number of chromosomes of their nuclei is halved by cell division (from $2n$ to n). Each of the many cells in the pollen sac, with this reduced haploid nucleus, surrounds itself with a thick wall. Thus a grain of pollen is formed, and its contents usually undergo division.

In the nucellus, on the other hand, where only four haploid cells result, one of these

Fig. 9 (on facing page). Many flowers that pass unnoticed contain hidden marvels, such as the woodland weed, the woodrush. This picture shows its 3 petals and 3 brown sepals, 6 stamens and the central green pistil. (Photo Lod).





Fig. 10. The flower of a cherry-tree in section, showing the sepals, petals, stamens and style (slightly nicked at its base by the razor). (Preparation by Nitsch. Photo Lod).

(6) Orthotropism: growing vertically, under the influence of gravity.

(7) Nycthemeral rhythm: rhythm due to the alternation of nights and days.

(8) Protandry; protogyny: in protandry, the male sexual elements ripen before the female ones. In protogyny the reverse occurs.

(9) Clone: a group of living organisms, which have all arisen from one individual, by vegetative reproduction.

multiplies *in situ*, while the other three disintegrate to form the embryo-sac.

In certain cases, however, several of the original four haploid cells multiply together and form the embryo-sac.

The male reproductive cells (σ gametes) originate in one of the pollen grain nuclei. There are two of them, formed by the nucleus dividing when the pollen germinates. Some only of the nuclei or cells of the embryo-sac act as female (f) gametes.

However this may be, it is at the time of meiotic division that inherited factors are distributed to the reproductive cells. Furthermore, there is a significant difference in the fact that there are numbers of haploid cells in the pollen grains and embryo-sacs, in contrast with the diploid state (with $2n$ chromosomes) of the rest of the plant. The special nature of these groups of cells with reduced nuclei is recognized by the term gametophyte applied to them, either male (pollen grain) or female (embryo-sac).

The f gametophyte is not shed, unlike the pollen grains, which may be scattered over

great distances. σ gametes are brought into contact with f gametes by pollen tubes, which grow out of the σ gametophyte formed when the pollen grains germinate. The tube has to follow a lengthy course to reach the f gamete, through the tissues of the carpel and the ovule, and is apparently guided by chemotaxis, and helped towards the ovum by two cells, the synergidae.

Fertilization and its consequences

The complicated fertilization mechanisms of Angiosperms were discovered by L. Guignard and S. Nawaschine simultaneously, at the end of the last century. Of the two σ gametes produced by a pollen grain, one unites with a haploid nucleus of the embryo-sac of the ovum, and produces a diploid fertilized egg-cell from which the embryo will be formed. The other gamete joins up with a nucleus formed out of the union of two haploid (polar) nuclei. The result is a triploid nucleus (with $3n$ chromosomes), which divides successively and forms a triploid reserve tissue, the albumen. This serves to nourish the embryo, when it is developing (ex albuminous seeds of the bean) or germinating (albuminous seeds of the castor-oil plant).

This double fertilization, however, besides initiating the formation of the embryo and albumen, also sets off the development of the other constituents of the seed, and that of fruit. The seed's state of suspended animation is due to the hardening of the ovule's skin, and the loss of water. The phenomena of differentiation which lead to the fruit's developing, occur simultaneously in neighbouring tissues, through the action of what are probably auxins. Parthenocarpy, ie development of a fruit without fertilization, can in fact be effected simply by the action of auxin (eg tomato), and it even occurs spontaneously in some varieties of cultivated plants (pineapples, bananas, and seedless grapes).

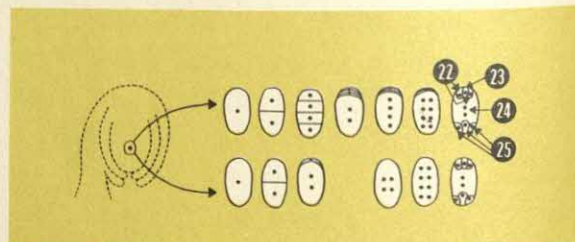


Fig. 11. Two ways in which the embryo-sac may be formed: only the original cell is diploid. (22: synergidal; 23: ovum; 24: polar nuclei; 25: antipodal cells).

Fig. 12. The flower of the scarlet pimpernel (*Anagallis arvensis*) shows that a shoot meristem can become either a vegetative meristem, producing leaves, or a floral meristem, producing flowers. The scarlet pimpernel never flowers when there are less than 8 hours' daylight, but a few bright days of longer duration are sufficient to transform axillary buds into flowers. If the bright light lasts for only 24 hours, and is followed by a period of short days, the process leading to flowering starts, and then, as it were, goes into reverse. Twelve days after the 24 hours' illumination, the plant was treated with gibberellic acid to accelerate the appearance of the proliferous flower. (Experiment by Mme Brulfert. Photo Lod).

Since fertilization reconstitutes the genetic material split up by meiosis, the significance of ♂ and ♀ gametes becomes obvious.

Bi-parental reproduction, the union of cells derived from two different individuals, provides a species with the greatest possible variability which may be obtained from the available genetic material, the significance of which is both immediate (adaptation) and future (evolution). Various adaptations facilitate this mode of reproduction: unisexual flowers, or those reaching sexual maturity at different times (protandry and protogyny),⁸ or inability of pollen to germinate on the gynoecium of the mother plant, etc.

There are also species in which self-fertilization (autogamy) is the general rule. As long as local conditions remain precisely the same, the genetic constitution remains limited for generations to a small number of genotypes, each of which reproduces itself exactly. This type of multiplication, although sexual, is equivalent to vegetative reproduction, as in a cutting, and it results in lines comparable with clones.⁹ In these strains, evolution or adaptation to new conditions can occur only as a result of accidental cross-fertilization or alteration in genetic constitution by mutation.

Finally, sexual reproduction leads to a change in the properties of cells, eg, in plants with several types of branch. In this case a seed from a plagiotropic branch always produces an orthotropic or more primitive type of stem first. This implies a degree of de-differentiation in the plagiotropic cell-type, which must have occurred at the formation of the gametophyte or gametes.

The general impression that we get from this brief summary of the life cycle of flowering plants is undoubtedly that of the complexity of the subject, for in spite of some remarkable discoveries, the reasons for many of the phenomena are still unknown; but it is surely in the cells that we shall find the answers.



Plant diseases

Hermon DARPOUX

Many diseases among higher plants are caused by fungi or bacteria. Some of these micro-organisms can live either as saprophytes¹ or parasitically, and they are called facultative parasites. Others have very strict requirements and have not yet been cultivated on artificial media; they are called obligatory parasites.

(1) Saprophytes: *non-autotrophic plants that grow on decomposing organisms, because they need organic matter for food. They may be contrasted both with autotrophic plants that need only mineral salts, and with parasitic plants that live on other living things.*

(2) Ectophyte: *a parasitic plant that lives on the surface of its host.*

(3) Endophyte: *a parasitic plant living inside its host.*

(4) Appressorium: *a swelling of the tip of the parasitic organism produced when contact is made with the parasitized cell.*

(5) Zoospore: *a spore which moves about with the aid of cilia or flagella.*

(6) Pore: *opening between the two cells of a stoma (see note 7, p. 71).*

Most fungi form spores to ensure their propagation. Wind, rain, insects, birds and man himself disseminate them—and also spread bacteria. Viruses, however, are usually transmitted by insects that bite (greenfly).

When fungal spores, or bacteria, reach a suitable host, contamination occurs if the conditions (eg, of humidity and temperature) are favourable. Some fungi are ectophytes,² such as the Erysiphaceae, which cause diseases called oidia. But most parasites are endophytes.³ Sometimes their entry into the host is passive, and the pathogenic agent penetrates the tissues on the site of an injury (eg, the white-rot of vines that follows a hailstorm). More frequently, however, penetration is active. Each of the spores of *Botrytis cinerea* (a grey mould) produces a thread that swells into an appressorium.⁴ This exerts pressure on the skin of the plant and thrusts out a sharp stylet that perforates it. This process is mostly mechanical, however; substances excreted by leaves which can stimulate or reduce the germination of these spores, have been isolated. The conidia of *Plasmopara viticola* (grape mildew) germinate in a drop of water and produce zoospores,⁵ which swim about

for a time and then attach themselves to the plant and put out threads that penetrate the pores⁶ of the air-stomata.⁷ The uredospores⁸ of *Puccinia graminis* (the black rust of the Gramineae) germinate on the plant's surface; the filament swells into an appressorium over a stoma, then extensions of it pass through the pore and form a vesicle in the space below the stoma, and the mycelium develops from this.

Some examples: the actinomycete *Streptomyces scabies* enters potato tubers by their lenticels; the bacterium *Pseudomonas campestris* gets into the leaves of Cruciferae by their water-stomata; the fungus *Ustilago tritici* penetrates wheat flowers by the stigma and the style; and *Plasmopara brassicae* makes its way into cabbages through their root-hairs.

Invasion by the parasite

The parasite then develops in the tissues of its host.

Many fungi are intracellular. They spread between membranes and send only their suckers into the cells (rusts, mildews). Scientists used to think that this action was purely mechanical, but it is now known that diastases

(pectinases, hydrolases, cellulases), secreted by the mycelium, may assist the action. For example, *Plasmopara viticola* forms pectinases which break down pectin compounds. Some fungi can cross membranes, eg *Pythium de Baryanum*, but others can progress only after killing the surrounding cells, at a distance, by means of the toxins they secrete; this is the action of *Nectria galligena*, the cause of apple and pear canker. Some fungi are typically intracellular, for example, the vegetative apparatus of *Synchytrium endobioticum* (wart disease of potatoes) is a plasmodium that remains inside the host's cells.

Phytopathogenic bacteria also act in several different ways. Most of them attack their host by digesting the middle layers of the cell membrane. The protopectins⁹ are broken down successively by protopectinases and pectinases; in some cases hydrolysis continues right to the stage of galacturonic acid which some bacteria use as a metabolite.

Other bacteria act by producing toxins. It has been shown that *Pseudomonas tabaci*, the causative agent of tobacco wildfire, secretes an exotoxin, an antimetabolite of methionine, which disturbs the metabolism of the latter and makes a ring round the point of entry. This toxin has been isolated and shown to be an amino-acid. Hydrolysis of it yields lactic acid and a fraction known as 'tab toxin', part of whose molecule is analogous to methionine.

Some pathogenic plant bacteria contain a polysaccharide substance that is responsible for their virulence. This has been demonstrated to be the case with *Xanthomonas phaseoli*, for example, which causes bean 'halo blight'.

A few bacteria produce forms of hyperplasia.¹⁰ The chief example is 'crown gall', which is due to *Agrobacterium tumefaciens*. The bacterium gains entry through the site of a recent wound. It spreads within the tissues and converts normal cells into malignant ones, which multiply rapidly and produce a tumour. Besides this tumour, which develops at the point of inoculation, bacteria-free secondary tumours or metastases may form elsewhere. Bands of tumour tissue have been shown to exist in the cortical parenchyma, and it appears that healthy cells are converted into tumour cells on the site of these abnormal bands (fig. 1).

Fig. 1. Following an injury, a bacterium, *Agrobacterium tumefaciens*, produces a kind of plant cancer. Two main tumours can be seen on this tomato-stem at either end of the wound, and some small round tumours which are newer. (Photo Lod).





Fig. 2. Streaks appearing on the flowers of a tulip are the result of a virus. The photograph shows two flowers of the same strain; the one without streaks is quite healthy. (Photo Darpoux, I.N.R.A.)

Tumour tissues contain a greater concentration of auxins than healthy tissues, but this does not adequately explain the process of tumour formation. The presence of the bacterium in the damaged tissue is known to be necessary to begin with, but once the process of tumour formation has begun, its disappearance does not prevent further growth. The optimum temperature for starting the process is 25–27°C; no tumour develops above 29°C. The active principle is therefore thermolabile, being destroyed as quickly as it is formed when the temperature is about 29°C. The energy required to initiate the reaction seems to be characteristic of the denaturation of proteins.

There are several theories about how tumours are induced:

(1) The active principle might be a virus carried by bacteria.

(2) It could be related to a deoxyribonucleic acid.¹¹ The virulence of different strains of *A. tumefaciens* has in fact been shown to have a connection with the presence of certain deoxyribonucleic acids.

Action of parasite on host

A parasite may produce either atrophy or increased growth of the affected organs, changes in shape and colour, or the death of tissues, organs, or the whole plant.

The main symptoms are: spots (an area of tissues becomes discoloured and then dies), mosaics (green and yellow patches on the leaves), crinkles (deformation of the edges of leaves), blights (part of the leaf swollen as a result of the hypertrophy of some cells), witch-brooms (chaotic development of certain buds, causing disorderly growth), galls (protuberances), tumours (localized growths caused by abnormal multiplication and hypertrophy of cells), necroses (areas of dead tissue), cankers (regions with a centre of dead tissue which becomes hollow, while the outer layers are hypertrophied and form swellings), wilting of part or whole of the plant, which occurs when its respiration is not balanced by its water intake, either because the parasite is obstructing the vascular channels, or because it produces toxins; and rotting, which appears when cells have died and become detached (fig. 3).

But these symptoms are only visible signs of the parasite's attack; numerous metabolic disturbances also occur within the host.

There is a marked increase in polyphenol-oxidase activity in most plants attacked by

parasitic fungi. Examples of this are potatoes infected with mildew (*Phytophthora infestans*), tomatoes carrying *Fusarium lycopersici*, and rice harbouring a *Piricularia*. This increased activity is often accompanied by higher concentration of the enzyme's substrates, which are compounds of phenol, chlorogenic acid (a caffeic acid-quinine complex) in particular. This change in the metabolism of polyphenol-oxidase and its substrates has also been discovered in plants affected by virus diseases.

The various viruses of tobacco plants (mosaic virus), potatoes (X, Y, A), hydrangeas, cherry trees and peach trees, all show that the polyphenol-oxidase activity in the plants, and also the concentration of phenol compounds, may be double those of healthy plants.

The products of oxidation of polyphenol (the quinones) are particularly toxic compounds. They inhibit the action of certain enzymes containing SH groups, and also the mechanism of oxidative phosphorylation.

Other metabolic disturbances among respiratory enzymes have also been found in plants affected by parasites; this is the case with peroxidase, catalase, cytochrome-oxidase and ascorbic acid-oxidase.

Research into inhibiting the synthesis of anthocyanin¹² pigments in plants affected by virus diseases, another aspect of metabolic disturbance, has recently begun. Many plants have variegated flowers. The tulip is the best-known of these, but stocks, pansies, gladioli, tobacco-plants, buttercups and anemones also have them. Detailed biochemical study of this phenomenon shows that the synthesis of anthocyanin pigments is inhibited while the virus is multiplying. Afterwards, the synthesis of pigments starts again, and it is then found that the anthocyanin content of the affected plants is almost the same as that of healthy plants, although there are large areas of discoloration in the former (fig. 2).

It appears that there is a point in common in plants between the metabolism of nucleic acids and proteins of one part, and that of flavone (anthocyanin) and phenol compounds of another part. Since nucleic acids and proteins play a fundamental part in processes that regulate cellular life, this research is obviously very important.

The plant's resistance to parasites

Plants have numerous mechanisms for resisting parasites' attacks. Sometimes their resistance is passive, for example, the thickness

of the skins hinders the penetration of *Botrytis*. In the same way the suberized periderm¹³ of the potato tuber stops *Spongospora*, the size and number of stomata stops *Pseudomonas citri*, and the hairiness of the leaves of pear and apple trees is an impediment to their parasites. Chemical substances in the superficial layers of cells also play a part. For instance, onions with brown skins, which contain quercetin and phenol compounds, resist the attacks of *Botrytis*, *Colletotrichum*, and *Fusarium*. Certain phenols, especially chlorogenic acid, which are present in the outer coverings of potato tubers, also help greatly to resist *Streptomyces scabies*.

In other cases the parasite is able to penetrate the host, but defence mechanisms hinder its spread. The membranes may resist perforation, eg, in the case of *Pythium*. Alternatively, the cytoplasm may contain antibiotics such as alkaloids, phenol derivatives, or heterosides, that prevent the parasite from developing. Absence of growth factors, which are essential to some obligatory parasites (rusts), may affect the issue; and the pH may be unfavourable to the parasite.

Some factors come into play only when the parasite starts acting upon its host, and this sort of resistance is active.

When the fungus *Nectria galligena* enters the branch of an apple tree, the host exhibits a wound reaction; cork-like barriers are set up to oppose the spread of the mycelium, and perhaps also the diffusion of toxins. Beads of gum are formed when a poppy is attacked by *Pyrenophora calvescens*.

Certain plants use hypersensitivity as a mechanism that they frequently operate as a resistance against obligatory parasites. The cells invaded are so sensitive to the action of the parasite that they quickly die, before it has time to extend. Being unable to continue living in a lifeless medium, the parasite also dies and the infection ends.

For instance, in the case of rusts, a sucker kills the cell immediately it penetrates, probably by producing a toxin. The mycelium may continue to produce suckers until the spore's reserves are exhausted. The parasite then dies after having killed only a small group of cells.¹⁴

Acquired immunity, so important in the animal kingdom, seldom occurs in plants, where there is no definite evidence of antibody formation. Some substances that agglutinate certain bacteria have been found in the potato; but they do not appear to be formed as a reaction to the parasite.

Phenomena resembling immunization,



Fig. 3. Rotting of the apple is due to a fungus *Monilia fructigena*. (Photo Cornuet, I.N.R.A., Versailles).

have, however, been observed with viruses. If a plant is inoculated with a strain of low virulence the disease produced will not be severe, and the plant will thereafter be protected from attack by more virulent strains of the same virus. The immunity so produced is specific and it occurs only between closely related strains.

Biological interference

Relations between host and parasite depend not only on the direct action of the physical and chemical factors of the environment, but also on the living world surrounding them.

There are a number of fungi and bacteria which attack phytopathogenic agents; these are called 'hyperparasites'. For example, fungi of the genus *Ciccinobolus* develop in the mycelium and spores of Erysiphaceae, causative agents of oidia; others of the genera *Darluca* and *Tuberculina* and a bacterium (*Xanthomonas uredovorus*) destroy the fructifications or uredinales, which cause rusts.

Bacteriophages, which are thought to be ultra-viruses, may break down bacteria and so reduce their phytopathogenic action.

(7) Stoma: the respiratory organ of a leaf, formed by two cells between which there is an opening, the pore.

Air-stoma: a stoma which lets in gas, in contrast to a water-stoma, which lets in water.

(8) Uredospore: red spore of the rust-fungus (a parasite), which germinates in summer (in contrast to teleutospores, black spores that hibernate, and then germinate in the spring).

(9) Protopectin: the precursor substance from which plants make pectins.

(10) Hyperplasia: excessive proliferation of cells.

(11) Deoxyribonucleic acid (DNA): an acid in cell-nuclei that carries hereditary characters.

(12) Anthocyanin pigment: the pigment that gives flowers their red or blue colour.

(13) Periderm: the scar-tissue that replaces the epidermis of an injured plant. Suberized periderm: periderm containing material similar to cork.

(14) Plants may conquer a parasite by the alterations that it provokes in their metabolism. The increased formation of phenolic compounds, which are oxidized to markedly toxic quinones, can lead to the death of the parasitized cells and to resistance by hypersensitivity. There are other examples where altered phenol metabolism, while not leading to such extreme results, still helps towards developing immunity. The tissues of a potato infected with *Helminthosporium carbonum*, for example, accumulate chlorogenic and caffeic acids in sufficient quantity to inhibit the development of the fungus completely. Another case described is that of *Endothia parasitica*, the cause of chestnut blight. This fungus forms adaptive enzymes, which break down the tannins and phenols that are toxic to it.

Certain insects (Coleoptera, Diptera) feed on fungi harmful to cultivated plants (blights, rusts and mildews), so that they may limit them quite considerably.

Phenomena of antagonism are also very common. These have been studied during the last few decades, together with the new research on antibiotics. It was found that when two micro-organisms were inoculated on a culture medium, one of them often had an adverse effect on the growth of the other. Many micro-organisms (bacteria, actinomycetes, or fungi) have this effect upon phytopathogenic agents. Several different mechanisms may be distinguished: spatial antagonism, where one organism's vigorous growth hinders the other's development; physical and chemical changes in the environment (certain fungi of the genus *Aspergillus* acidify the medium and make it unsuitable for the growth of other organisms); competition for the available nourishment; and the production of antibiotic substances by the antagonist.

The microbe population of the soil is enormous, and a gram of earth may contain several million actinomycetes, bacteria and fungi. Quite a high proportion of these micro-organisms are antagonistic to phytopathogenic agents when cultivated on artificial media, and they also play an important part in natural conditions. It is possible to encourage their growth and so reduce the ravages of certain diseases by modifying the medium, for instance by adding green manure, organic substances, or trace elements, by altering the acidity, or by chemical treatment. For instance, carbon bisulphide favours the growth of a *Trichoderma* antagonistic to *Armillaria*, which causes root-rot in fruit trees.

The action of antagonists in the soil is similar to the results displayed *in vitro*, but it should also be mentioned that an increase in carbon dioxide concentration is inimical to certain parasitic fungi such as *Sclerotinia*. The production of antibiotic substances in the soil is slight, but it can be increased by the addition of certain nutrients. Most antibiotics are rapidly put out of action either by adsorption on the soil colloids (streptomycin), or by diastases secreted by micro-organisms (penicillin). But there are some, such as chloromycetin, which are stable enough to play a biological role.

Phenomena of antagonism also occur in seeds. Superficial chemical treatment, eliminating only saprophytes on the surface, may encourage parasites buried beneath the coverings of the seeds to grow.

Antagonists can also prevent the establishment of wound parasites in organs above ground; they may also stand in the way of those that develop in a living host after colonizing dead tissues. *Stereum purpureum*, the fungus that causes silver-leaf disease in fruit trees, finds it difficult to penetrate old lesions already colonized by saprophytes. *Botrytis*, which establishes itself on the dead petals of the tomato and then attacks the fruit, is considerably impeded if the petals are sprayed with a suspension of *Cladosporium* or *Penicillium* spores.

Antibiotic substances

Antibiotics are substances produced by living organisms, and their action is inhibitory or lethal. Most antibiotics used in medicine to treat infectious diseases are secreted by micro-organisms, for instance, penicillin by the fungus *Penicillium notatum*, streptomycin by the actinomycete *Streptomyces griseus*, and subtilin by the bacterium *Bacillus subtilis*.

Antibiotics can also be formed in the tissues of higher plants, which excrete some of them, particularly by their roots. They may help the plant to resist a parasite, and they also have an influence on the surrounding microflora.

The way many antibiotics act on both phytopathogenic agents and the host plant has been studied. Many of them do act against fungi or bacteria *in vitro*. Attempts have been made to employ them against certain plant diseases, and successful results have been obtained in disinfecting seeds and treating parts above the ground. Some antibiotics are now known to have antiviral properties: trichothecin and others prevent the virus from obtaining a foothold on the plant, while terramycin and aureomycin partially stop it from multiplying.

Some antibiotics can be absorbed by the roots of plants; thus streptomycin enters the tissues of a young cucumber plant and penetrates into the parts above ground while its roots are immersed in a liquid medium containing the antibiotic. But under natural conditions, absorption is negligible because the soil inactivates the antibiotic, so that parts above ground absorb only very small quantities.

Many antibiotics are phytotoxic and induce necrotic lesions (alternaric acid, actidione, trichothecin), chlorosis (large doses of streptomycin), or withering (lycomarasmin), frequently followed by the plant's death.

In small doses, some antibiotics seem to stimulate plant growth.

Internal regulatory mechanisms

A stump of chicory root, when placed in a damp atmosphere, grows buds at the apical pole and roots at the basal pole. If the stump is cut into smaller pieces, each fragment forms buds at the apical pole and roots at the basal pole. (Photo Lod).



Plant growth

Kenneth V. THIMANN

When a baby grows up to become a man, all its parts enlarge almost equally—the tiny hands and feet, the length and breadth of the back, the lungs and the liver, even the head (though the head may enlarge a little less than the rest). Thus the proportions of the different parts and organs do not change much during growth. With plants it is entirely different.



Fig. 1. A plant embryo, in contrast to an animal embryo, bears no resemblance to the adult. This embryo of *Pseudotsuga taxifolia* hardly suggests a fir tree. (Photo Lod).

The embryo as it first develops from the fertilized egg is a simple structure, a tiny root and shoot, bearing one or two 'seed leaves' or cotyledons, but no other organs. After growing for a while it stops, when we consider the seed to be 'mature'. The embryo, fully formed, is then in a relatively induced state of desiccation in which it can survive for months or years. Very often, as in wheat or the bean, the one or two cotyledons are swollen with stored starch or proteins, which are destined to be used as food by the young embryo later on.

When the seed is planted and growth consequently begins again, a curious and characteristic pattern develops: the tips or apices of both the root and the shoot seem to take over the control and direction of the growth. This is seen both in structure and in function.

In the root the cells just behind the tip begin to divide rapidly, and the resulting small cells push out lengthwise to form that long thin cylinder which is characteristically the image of a root. The elongation of these cells, of course, pushes the tip farther away and the new cells of the tip, in their turn, begin to elongate. Soon the elongating cells are 3 to 5 mm behind the tip and at this time their growth slows down; presently it stops altogether. Meanwhile, other cells nearer the tip

are carrying on the elongation process until they too become far enough back to be fully extended and in their turn cease elongation. Among these cells which are fully grown and some millimetres from the tip, there develop at a certain number of specific spots newly active cells which begin to divide and form local masses of tiny cells. But these now elongate, not in the lengthwise but in the crosswise direction, to produce new rootlets growing out at right angles to the parent root. Apparently the presence of the tip of the parent root slows down this formation of new rootlets, for if the tip is cut off the rootlets appear sooner and often in greater numbers.

A pattern differing in detail but comparable in principle can be discerned in the shoots. Here it is the cells in the extreme apex¹ itself, especially those in the outermost layer, which divide rapidly to produce a number of tiny cells, and when these enlarge some do so in one direction and some in another. Those which enlarge superficially, that is over the surface of the shoot tip, cause it to form into folds, and these folds grow out to produce little thin triangles which are the beginnings of leaves. The cells in them continue to divide and elongate until the characteristic broad flat leaf structure appears. After a while the cells near the tip of the leaf slow down their growth

while those at the margin and especially towards the base continue to divide and enlarge. By variations in the location and timing of this slowing-down, the different leaf forms, so characteristic of different plants, are generated.

Meanwhile other cells formed from the continuing divisions in the apex, enlarge along the lengthwise direction of the shoot, pushing the apex forward in front of them just as in the root. Thus at a little distance behind the apex we see long narrow cells and it is these which form the elongating *stem*. As the apex is pushed ahead, one by one the leaves get left behind. Now a new phenomenon appears; at the extreme base of each leaf there is again a little nest of dividing cells and presently, as the apex gets farther and farther away, these may divide and elongate to form a new branch shoot similar to the main apex. Again as in the root this formation of branches is greatly delayed by the main apex, and sometimes indeed it is prevented almost completely—witness the very long unbranched stems of such plants as the sunflower. If we cut off the apex, branching begins at once, often at the first leaf below the apex.

Thus in both root and shoot the pattern is: (1) the formation of a nest of rapidly dividing cells (called by botanists a meristem); (2) the enlargements of these cells lengthwise to form a long cylindrical structure; and (3) the regular throwing-off, at some distance below, of lateral organs, to the extent allowed by the control exerted from the tip. In the shoot, in addition, there is the production right in the tip itself of another set of lateral organs—the leaves.

Changes in the cells during growth

As the pattern of the plant develops, the cells which compose it are constantly changing in their appearance and structure. While they are rapidly dividing they show large nuclei centred in a mass of cytoplasm. Throughout this cytoplasm there are tiny structures of five or six different types; these fine particles or vesicles are the subject of very active research at the present time and it is clear that each has its own very specific function to perform in maintaining the cell's activity and growth.

Fig. 2. The cells of the young root tip divide actively, as shown in this specimen of an onion root. The chromosomes can clearly be seen in the various stages of mitosis. (Photo Lod).



(¹) Apex: farthestmost tip of the stem.

When the cells begin to enlarge, vesicles of one of the types fuse together to make a large lake of watery solution in the cytoplasm. The nucleus retires to one of the sidewalls and the lake of solution, called the *vacuole*, enlarges greatly, so that it comes to occupy more than half the cell's volume. The containing cell enlargement is thus in good part due to enlargement of the vacuole. The other bodies in the cytoplasm undergo changes too, depending on the functions the cell is to perform. Some of these changes are too complex to discuss here, but one is particularly prominent: in cells which are going to form leaves or the outer layers of green stems, one type of particle enlarges and a tiny granule inside it turns green. The granular matter expands almost explosively and in a few hours it fills the enlarging vesicle with a closely packed mass of green layers. This whole green body is now called a *chloroplast*, and its green pigment, chlorophyll, is the agency which captures the energy of light, to convert it into the chemical form of the energy of sugar and of all the other substances of which the plant body is composed.

The cell wall

One other feature of plant cells plays an important part in growth: the wall. The cells of animal tissue are usually soft and devoid of characteristic shape, except those which form long fibres as in muscle and nerve. But the cells of plants bear a firm wall on the outside, of characteristic geometrical shape. This wall is formed of a padding of tiny fibres closely intertwined. One of the major constituents is cellulose. It is these outer walls which supply the fibrous materials of commerce, such as paper, cotton, linen and jute. Their tough, hard, inextensible nature gives them most valuable properties as textiles. Yet it raises a most difficult problem in visualizing growth, for if the cell enlarges, its wall must enlarge too, and therefore these walls, however tough they seem in our textiles, must be very readily expansible when they are *in situ*. It has been found in recent years that these walls are not, in fact, simply stretched by expansion of the cell contents, but that they are constantly being added to and modified by the activity of enzymes in the cytoplasm. Cell enlargement, indeed, is dependent on oxidation, which supplies energy for chemical changes. This will be discussed further in another section.

When the cells have completed their enlargement and the wall therefore need no

longer be extended, it changes its character very drastically. New chemicals are laid down in between the particles of cellulose and the other softer materials. New and thicker layers are often laid on until at last the wall fills up much of the cell and the cytoplasm inside dies. This is typical of what happens in woody stems, for example, in the trunks of trees, where about half the weight consists of the chemical *lignin*, which has been inserted into the cell walls, and laid on top of them, after growth has stopped. Such cells with greatly thickened walls are almost always dead. The resulting *wood* has, of course, tremendous importance in man's varied activities. In some other kinds of cell, instead of lignin the thickening is of the same cellulosic material as the original wall. It is to this type that cotton fibres belong.

All these changes to the cell wall are to be considered as essential parts of the totality of changes which occur in cells as they mature and become different in functional type. The whole process is referred to as *differentiation*. Some botanists use the terms *meresis* for cell division, *auxesis* for enlargement (growth in the ordinary sense of the word) and *maturation* for all those changes which go on when the cell has stopped growing.

How are these regular patterns of growth maintained? The plant has no circulation comparable to that of the blood of animals, which acts to integrate all the activities of the animal body. As we have seen, growth is rather a localized phenomenon in plants, occurring in some areas and not in others, and generally for only a brief time in each part. Correspondingly the control of growth is localized and changes with time. We shall see below that the most important method of control, the understanding of which has come from the most modern researches on plants, is that of the secretion of *growth-controlling substances*, which move from cell to cell, generally over only short distances. Commonly they are secreted by growing tips. These substances have a multitude of functions. Changes in the cell wall, without which no enlargement could occur, are induced by them. When the tip of a shoot influences the formation of branches lower down, that influence is transmitted by a growth substance secreted by the tip. Even cell division is under the control of growth substances, to which some cells respond more readily than others. Because these substances are formed in one part of the plant and transmitted to another part, where they exert their function, they act as chemical messengers and belong to the class of *hormones*.

Polarity, correlation and grafts

Paul CHAMPAGNAT

The physical concept of 'polarity' has been extended, by analogy, to plants. Just like a magnet, or an electrical generator, most plants have two poles possessing different properties. This is such common knowledge that no one is astonished to find that a seed contains an embryo made up of a leaf bud, representing the leaf pole, and a radicle or small root, representing the root pole.

The idea of polarity is most easily visualized not by considering the whole plant, but pieces of it. If portions of willows cut from between nodes, or sections of chicory root are placed on wet sand, we can watch newly-formed buds growing from the part which was originally nearest to the apex of the stem, or the top of the root. The new roots, on the other hand, appear at the other end of the section. Thus a stem possesses a root pole, and a root possesses a leaf pole.

Polarity in plants

This property does not depend on the size of the cutting. Vöchting was the first to point out that even very fine slices often produced regenerating buds and roots which were as strictly localized as the ones on larger pieces. In the same way the smallest pieces taken from the magnetized needle of a compass will show the same north-veering property as the whole needle. It can be thought, therefore, that every single cell in a plant is polarized. In fact this is what we find in single cells taken, for example, from filamentous algae, where the plant has neither stem nor roots, so that one end produces a rhizoid to fix it down, and the other a filament to assimilate nourishment. Thus the term polarity is applicable whenever two parts of a cell, or of a group of cells, have a different destiny.

However, the mother cells of gametes or spores, and the ova immediately after fertilization, are not polarized, although they themselves have been produced by normal cells. This loss of polarity, the mechanism of which is as yet unknown, does not last long and is repaired before the first mitotic division. Many widely different factors in the environment can at that time induce this polarity.

It will remain labile for several hours but after that, as we shall show, it becomes practically irreversible. At first an *Equisetum* (horse-tail) spore has a central nucleus with the chloroplasts distributed evenly around it. If it is exposed to light from one side, the chloroplasts migrate to one pole and the nucleus to the other. A mitotic division then occurs, with the equatorial plate at right angles to the direction of the light beam, so that two cells of unequal size are formed. A polarity has been produced under the influence of light. In a similar way a temperature gradient, variations in acidity, or a difference of electric potential may act as inducers. Among the *Archegoniates*¹ the maternal tissues surrounding the gametes and the fertilized ova determine the polarity. It is for this reason that the ovum and the synergidae of an embryo-sac are always close to the micropyle² of an ovule, whatever the ovule's position is in relation to the force of gravity.

The example of the horse-tail spore shows that a polarity is accompanied by protoplasmic changes. This phenomenon may be due to the cytoplasmic proteins becoming arranged to form some kind of orientated structure. Research is needed to provide evidence to support this hypothesis. This cytoplasmic polarity could afterwards allow the transmission of certain influences within the plant, and the movement of certain substances in a predetermined direction; just as a train travels from one station to another along rails laid end to end, but cannot do so if the rails are left scattered about. The origin of different organs in different parts of a cell or axis, results. It must be realized that once acquired by the egg-cell such structures are transmitted to all the daughter cells.



Fig. 1. The apical pole always tends to produce buds, and the basal pole, roots, as we see in the willow cutting on the left. If the cutting is turned upside down the buds continue to form at the true apical pole and the roots at the true basal pole. (Photo Lod).



Fig. 2. Two extreme examples of variation of apical dominance in herbaceous plants. Right: total apical dominance (except at the very base of the new branch) in *Euphorbia lathyris*. Left: no dominance (all the lateral buds have sprouted) in *Galinsoga parviflora*. (Photo Lod).



Fig. 3. Cuttings of the lateral branches of *Araucaria excelsa* never straighten up again, but keep their tendency to grow in a horizontal direction. (Photo Maresquelle, Strasburg).

It is very difficult to eradicate or reverse a natural polarity, although many research workers have claimed to have done this. Let us examine two examples:

(1) Roots or buds have been obtained at either end of cuttings from the root of the chicory or the dandelion (Warmke and Warmke). To do this it suffices, in the first case, to increase the auxin content of the cutting by applying β -indolylacetic acid and, in the second case, to diminish it by rendering inactive or destroying the natural growth substances (fig. 7). But the cytoplasmic polarity has not in fact disappeared, for if we take a root segment which has been made to produce either roots or buds, and we then cut off the two ends with the organs they have produced and put the cutting back on wet sand, it will produce both buds and roots in the normal position without any further treatment.

(2) *Bryopsis* is a green alga which has rhizoids at the bottom to fix it down and near the top some 'branches' with chlorophyll which look rather like the barbs of a feather. This structure is called coenocytial³ because it is not divided into cells by partitions. If one of these organisms has its two ends cut off and is planted upside down in the sandy bottom of an aquarium, a rhizoid will develop at the pole originally concerned with assimilation, while chlorophyll-containing 'branches' will appear at the end which previously bore the rhizoid. This is not, however, an inversion of the polarity, since the cytoplasm is seen to

turn, in a way, within the membrane before any regeneration occurs. At the moment that the segment is planted upside down, the chloroplasts are numerous at the end placed in the sand, while there are none at the opposite end. After being planted they very quickly migrate to the other end, or rather, as Steinecke showed by using dyes, the whole of the cytoplasm moves round, much like a giant amoeba. The membrane of the former fixing end now contains the cytoplasm from the assimilating end, so that it is quite natural that the chlorophyll-containing 'branches' should be produced here. However, theoretically, a modification of cytoplasmic polarity is possible since it does disappear in the mother cells of spores and gametes.

Polarity is also the most important factor in differentiation, for without it the ovum or spore would not produce the multiplicity of tissues and organs which make up the adult plant. For example, we can treat a moss spore with colchicine or chloral hydrate to prevent its acquiring polarity, with the result that, instead of getting normal filaments on which leaf buds then appear, we get a formless mass of similar cells. In the same way the cells of certain tumours proliferate wildly, without differentiating and without forming a definite tissue, because they have lost their polarity for some reason which we do not yet understand. This may well be an important stage in the origin of a cancer.

Finally, polarity is a factor in regulating the form of the plant: the organs do not appear at random. It initiates and facilitates the co-ordination between cells or between organs that will now be described.

Correlation

The organs and cells of plants do not behave as independent units; on the contrary they all influence each other in very varied ways, by means of mechanisms that come under the heading of correlation. There are two possible ways of showing their existence. One is to cut off part of a plant and observe both the behaviour of the isolated organ and the results of its removal on the remaining parts. The other is to introduce a new organ into a plant or part of a plant, and to see what happens to it. Grafting (which will be discussed in the next section) is an example of this method.

Other manifestations of correlation are less visible. For example, the younger leaves on a terminal bud inhibit the growth of older leaves. Isolated leaves, apparently adult, begin

to grow again when used as cuttings, while the presence of buds and leaves on cuttings stimulates the formation of roots. If the new roots on these cuttings are removed as soon as they appear, a much greater number of roots will be obtained, and they will go on appearing for a longer period. Thus the total number of roots produced depends, not only on the stimulation from the leaves, but also on inhibitory correlation acting between the first roots to be formed. The same thing occurs with the formation of tubers on a potato plant. Another case of inhibition is shown by cutting off the apex just above an oblique branch of spruce, which will then straighten up to replace the lost apex, so that its previous oblique growth must have been due to dominance by the apex. In other conifers, such as *Araucaria* (monkey-puzzle), horizontal branches are unable to straighten up, and if they are made to grow as cuttings they keep their 'plagiotropism' (fig. 3). In this case a new bud replaces the lost apex.

The diversity of such phenomena suggests that there are also many underlying mechanisms. In certain cases the competition of less explained trophic forces may be envisaged. For example, if severe pruning of the roots of a fruit tree influences the growth of the branches, the reason is that the quantity of the minerals supplied to the aerial parts of the tree is diminished because the absorption is less.

In other cases it seems that a hormonal mechanism is at work. Buds stimulate the growth of new roots by means of substances which they synthesize and which diffuse in the direction of the cellular polarity. The fertilized ovum permits the fleshy parts of the fruit to swell because of the auxin which it produces in the embryo and the albuminous part of the seed. Nitsch, in an ingenious experiment, has replaced the achenes of the strawberry by adding hormones; he had shown previously that the fruit swelled only if these achenes were present.

The correlation between buds has been studied extensively but the mechanism has still not been entirely clarified. The present theory is that the fate of a bud depends on a balance between two influences: (1) a hormonal inhibition coming from the dominant apex and (2) stimulation capable of overcoming this inhibition, which some sugars, kinetin, the gibberellins (see the following chapter) and certain vitamins can do. The decapitation of a plant abruptly lowers the level of inhibition and the stimulators induce the growth of buds.

If these are abundant, or if there is not much of the inhibitor, then branches will even grow in the presence of the apex. We can see, therefore, that there may be many intermediate stages between stems with many branches and those where only the terminal bud is actually developing.

Correlation is essential to plant life for it prevents morphological anarchy in the intact plant by inhibiting the cells from developing all their potentialities to the full. Since these potentialities are only masked, they can reappear and enable organs or tissues to be regenerated if the plant is damaged. The specific repartition of tissues and the number, development and orientation of organs are controlled by correlation. In fact correlations largely determine the general appearance of the plant. They are manifested either by growth stimulators, or more frequently, by growth inhibitors, which are often hormonal

(1) Archegoniates: a group of plants possessing archegonia. The archegonium is a bottle-shaped multicellular organ. The lower part contains the female cell (the haploid ovum) which will be fertilized by a male nucleus. Archegonia are found among the Bryophytes (mosses), Pteridophytes (ferns), Gymnosperms (conifers) and Angiosperms (flowering plants).

(2) Micropyle: the mouth of the ovule in plants.

(3) Coenocytial structure: a structure in which several cellular nuclei are present, not separated by membranes.

(4) Cambium: a growing zone between the wood and the bast (phloem), made up of actively dividing cells.

Fig. 4. Correlation in *Bidens pilosus*. The decapitation of the apex of a young plant leads to the development of buds placed in the axils of the leaves. If the left leaf is removed the left-hand bud takes precedence over the right-hand one. (Experiment by Champagnat).





Grafts and chimaeras

The grafts which are of most practical interest are usually those of buds, but in fact one can graft a great variety of organs, such as flower buds, or isolated leaves and roots. Vöchting has even succeeded in grafting two fruits together, and a fruit or a whole plant to an isolated leaf. It is also possible to unite fungi, algae and mosses. It is essential, for bud-grafting to be successful, to achieve union of the two partners. Each begins by producing a callus at the site of wounding, which is formed by actively dividing cells, usually derived from the cambium.⁴ These cells mix together and stick firmly to each other. Then some differentiate into the vessels of the wood and others into sieve-tubs of the phloem or bast, which unite the conducting tubes of the graft to those of the host. This explains why experts insist that it is necessary to put one active cambium in contact with another when making any graft.

But contact by itself is not enough, and there are two other conditions which must be fulfilled:

(1) There must be sufficient affinity between the partners, that is they must have close chemical, physiological and organic analogies. Affinity is closest of course when an organ is replaced on the plant from which it has just been removed. It is often satisfactory when the two plants are closely related, but there is no absolute rule, and some species which are botanically very closely related cannot be grafted, for example, apple and pear, while others from quite different families or genera unite easily, such as pear on quince, olive on lilac and bay on Saint Lucia cherry. The reason for this is not at all clear.

(2) The polarity of the cells in the graft must be the same as that of the host. A root pole easily unites with a leaf pole, but never with another root pole. In some cases it has been possible to make grafts with a reversed polarity tube, but the 'individuals' so formed

Fig. 5. In 1829, a nurseryman, Adam of Asnières, grafted a bud from the purple-flowered laburnum (Cytisus purpureus) on to a laburnum of the usual yellow-flowered species (Cytisus laburnum). The result seemed to be a new species which was given the name of Cytisus Adami. However, there had not been any hybridization in the true sense of the term, but a 'chimaera' had been formed, that is, a plant containing a mixture of cells from the two original species. The branch of Cytisus Adami in the photograph shows a bunch of yellow flowers on the same branch as the purple ones; this phenomenon is due to the cells of Cytisus laburnum dissociating themselves from the complex. (Photo Lod).

are always very feeble and need constant care if they are to be kept alive for a few months or at the most a few years.

The combination of graft and host after union can be considered as one individual, for one has adopted the roots of the other, and the latter the stem of the former. This is proved by the fact that neither attempts to replace its own missing organs, as it would do if it had not been grafted.

Grafting, as well as providing a method for studying correlation, provides irrefutable evidence of its existence and importance. So it is not surprising when the same variety of apple is grafted on to hosts of different vigour, that the vigour of branch-growth varies with that of the stock (host). This is because of the correlation between the aerial branch system and the subterranean root system. We also know that grafting is the best way of demonstrating the stimulating effect of leaves or buds on the production of roots; in this case the union does not have to be complete.

Multiple exchanges occur between two partners in a graft, but nevertheless the graft and the host maintain most of the peculiarities of their own metabolisms. A variety of vine which bears white grapes when grafted on to one with red fruit does not acquire the power of synthesizing the anthocyanin pigments of the host. And we shall not find new sugars, or more sugar, in a fodder beetroot grafted on to a sugar-beet.

Most originators consider that a graft cannot modify the hereditary make-up of a plant. On the contrary, it is the very best method of preserving the characters of unstable hybrids such as dessert apples and pears, and seedless varieties, such as oranges. Most of the graft hybrids which have been described are in fact chimaeras, that is to say there is a juxtaposition of the cells of the two partners, each keeping its own characteristics. It is very easy to understand how chimaeras are formed. When a graft that has made a perfect union is cut through the point of junction, active cells will begin to multiply, and new buds may appear on the callus so formed. If one of them starts growing along the side of junction and includes a group of cells from each of the species, the resultant branch will be a 'sectorial' chimaera. Another type of chimaera is called 'periclinal' (fig. 6). In this the cells of the one species completely cover those of the other variety in the growing point, forming a layer of variable thickness. Since it has a mixed origin it will appear to be a hybrid, which explains why it is sometimes called a 'graft hybrid'.

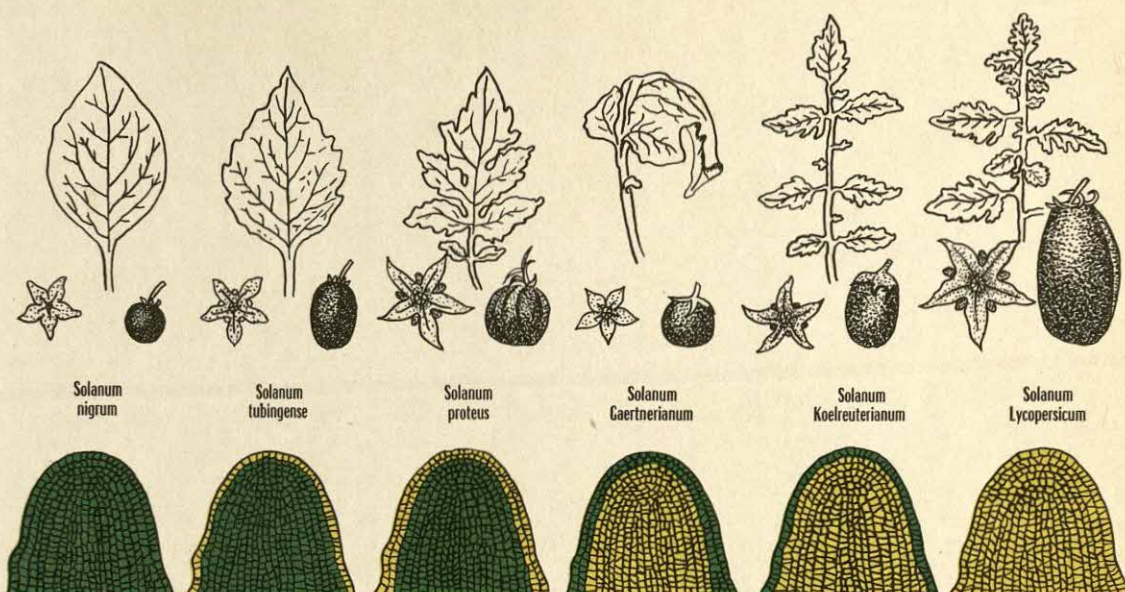


Fig. 6. Diagram of a series of periclinal chimaeras between the black nightshade (left) and the tomato (right). The illustration shows a leaf, a flower, a fruit and a diagram of the vegetative apex, for each 'graft hybrid'. The tissues of the tomato are shown in yellow, and those of the black nightshade in green. (After Winkler).

A periclinal chimaera can easily originate from a sectorial one. The area of contact between the cells of the two species is irregular, and those of one may penetrate to a slight depth beneath the epidermis of the other. If a bud originates at this point it will develop covered with a layer of cells of the second species. There are also chimaeras which are not derived from grafts but from somatic mutation or localized polyploidy, where again the cells of different genetic constitution form a mixed plant without losing their own hereditary characteristics.

This co-operation between two different elements is not particularly astonishing. Numerous examples of correlation are known to control the function of cells and the development of organs, and most of these are inhibitors. The different parts of a plant act on each other to prevent a state of anarchy, which would stop the plant from attaining its specific form and endanger its survival. The remarkable harmony of forms and structures is more the result of an 'armed peace' than the juxtaposition of ideal entities.

It is this state of competition and mutual sacrifice which makes possible and almost normal co-existence of and co-operation between cells or organs of different origins: a situation that brings to mind the world-wide inter-relationships between human societies.

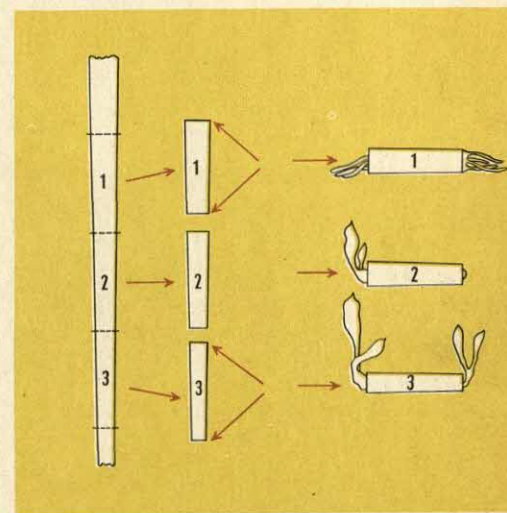


Fig. 7. Suppression of polarity in regenerating pieces of dandelion roots. 1 Increase of auxin in a piece results in production of rootlets at both poles. 2 Control experiment: note that the formation of shoots precedes that of rootlets. 3 Reduction of the quantity of auxin after treatment with ethylene chlorhydrin results in the formation of shoots at both poles. (After Warmke and Warmke).

Plant hormones

Jean-P. NITSCH

Inside an organism the question is whether such and such a nutritional element is directed towards cellular division rather than to simple enlargement, to formation of roots rather than buds, and to making leaves rather than flowers. The factors of organization and equilibrium which govern the structure and development of the plant are called 'growth factors', because their function is to regulate growth in all its forms. Some of these are stimulative and some inhibitory, like the accelerator or the brake of a car; the mechanism is extremely complicated but precise to the last detail.

Until the beginning of the twentieth century the nature of the factors concerned with organization and regulation remained a mystery. At one time the term 'vital force' was used and later, when electricity was discovered, it was drawn into the attempt at explaining the interaction of organs. Simple, precise experiments on particular points of plant biology were finally made, and these definitely demonstrated that growth is regulated by means of chemical substances.

The disease of gigantism

We shall consider three historic examples: the rice disease, called 'bakanae'; fruit growth; and the tropisms of the oat coleoptile.

The rice-producing countries, such as Japan, have long known a disease which has curious symptoms: certain small plants in the seed-beds grow taller than the average and take on a drawn-out, yellowish appearance like plants etiolated by lack of light. The Japanese have given the suggestive names of 'saginae' ('heron-plant') and 'bakanae' ('mad-plant') to these plants. It seems that they are worn out by this abnormally rapid growth-rate and are also poisoned by a substance known as fusaric acid, so that they finally succumb.

Japanese pathologists showed that the cause of the disease was a parasitic fungus, which they succeeded in growing on synthetic

culture media. But it was Kurosawa, in Formosa, who (in 1926) showed that the agent responsible for this gigantism was chemical. After eliminating the fungus from small rice plants by filtration and sterilization, Kurosawa applied culture broths. These sterile broths produced the same symptoms of gigantism as the parasite. Japanese chemists were then certain that the substance secreted by the fungus was chemical, and so they set to work. By chemical means they had to extract, isolate and discover the active principle. Their first efforts were not very fruitful. When they managed to crystallize one of the constituents of the extract, it turned out to be very toxic—fusaric acid in fact. But subsequently the elimination of this toxic product helped progress, and as a result Yabuta and Sumiki were able to announce (in 1938) the isolation of a definite chemical substance which by itself reproduced the symptoms of gigantism, just like the parasite. The parasite was called *Gibberella fujikuroi* and it was decided to call the substance 'gibberellin'.

The growth of fruits

In 1909 the German scientist Fitting was in Java, and his attention was attracted by the orchids, which are so bizarre and varied in form and colour. Fitting noticed that they faded rapidly once they had been pollinated,



Fig. 1. The application of a substance extracted from chrysanthemums which have been 'induced' to flower, produces upward growth and flowering (left). Gibberellic acid produces the same effect (right). (Experiment by Harada. Photo Lod).

and wondered if it was possible to find out anything more precise about this phenomenon. He tried to replace the orchid pollen by that of quite different species; with pollen from the hibiscus he obtained the same result: the petals wilted and the ovary began to swell, but in this case there had been no true fertilization. On continuing these experiments, he noticed that even dead pollen, incapable of activity, produced the same effect. Finally he made watery extracts of pollen and when these were applied to the stigmata of orchids the same symptoms occurred. Thus it was clear that the phenomenon was chemical.

Thirty-seven years later Haagen-Smit and his colleagues isolated a well-defined chemical substance, indole-3-acetic acid, from the immature caryopses of the maize plant. This acid has the property of making orchid flowers fade and fruit ovaries grow, even in tomatoes and other species—a second example of a biological phenomenon resulting from the action of a chemical substance.

The study of tropisms

The essential points of what may be called the science of plant hormones come straight from laboratory experiments on tropisms. It is well known that the stems of plants bend towards the light (positive phototropism) and away from the pull of gravity (negative geotropism). Thus when seeds of wheat are germinated in the dark, the germs that develop and which are protected by a sort of sheath, called the coleoptile, grow straight. If they are illuminated from one side, for instance by making a hole in the side of the dark box in which they are growing, the coleoptile bends towards the source of light. As long ago as 1880 Darwin showed with small cones of tinfoil that it was the tip of the coleoptile of a grass (*Phalaris canariensis*) which was stimulated by the light coming from one side, but that the actual bending was greatest at a point several millimetres below the region sensitive to the light. From this Darwin concluded that some stimulus must be transmitted from the tip to the tissues lower down. The nature of this stimulus was a cause of controversy among plant physiologists for many years. Among the suggestions put forward was one that the light produced a polarization of cells, and that this polarization was transmitted from one cell to another (Fitting, 1907), but this explanation was not borne out by experiments. In 1910 Boysen-Jensen showed that phototropic excitation could be transmitted even if the tip was cut off completely and then replaced on the

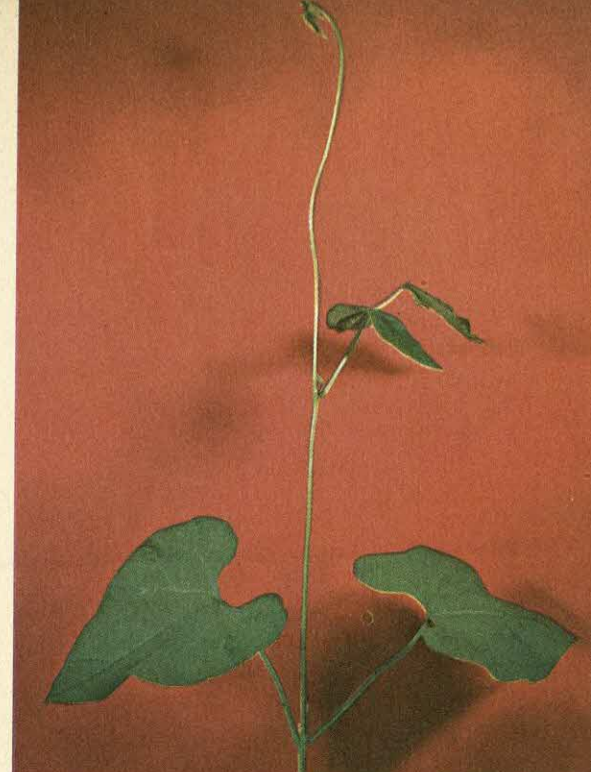


Fig. 2. These two heads of dwarf French bean have been cultivated under the same conditions and are of the same age, but a single spraying with a solution containing gibberellic acid (50 mg to the litre) was enough to stimulate the growth of the plant on the right and turn it into a runner bean.

coleoptile with a drop of gelatine intercalated between. This showed that the stimulus must be chemical. The famous physiologist, F. W. Went, perfected a quantitative technique for the detection and measurement of growth substances in the tips of coleoptiles (fig. 3). First of all he showed that when a coleoptile tip was cut off and placed on a small cube of agar gel (obtained by dissolving 2 per cent of agar in boiling water and allowing it to cool), it diffused something into the cube. The living tip could then be thrown away, as the cube of agar had acquired its properties. If the cube was fixed to one side of the top of a decapitated coleoptile, after one or two hours it bent away from the side to which the cube was fixed, because growth was more vigorous on that side. Went measured the angle of curvature so obtained and established that it was proportional to the number of coleoptile tips which had been placed on the agar cube in the first place. The resultant growth was therefore proportional to the quantity of the substance which had diffused into the agar.

This test, perfected by Went, opened the way for the quantitative study of growth substances; with it their presence in numerous organs can be detected and measured. Chemists also can undertake the task, which is both difficult and delicate, of extracting and isolating them; for example, Haagen-Smit and his colleagues used this test to isolate indole-3-acetic acid.

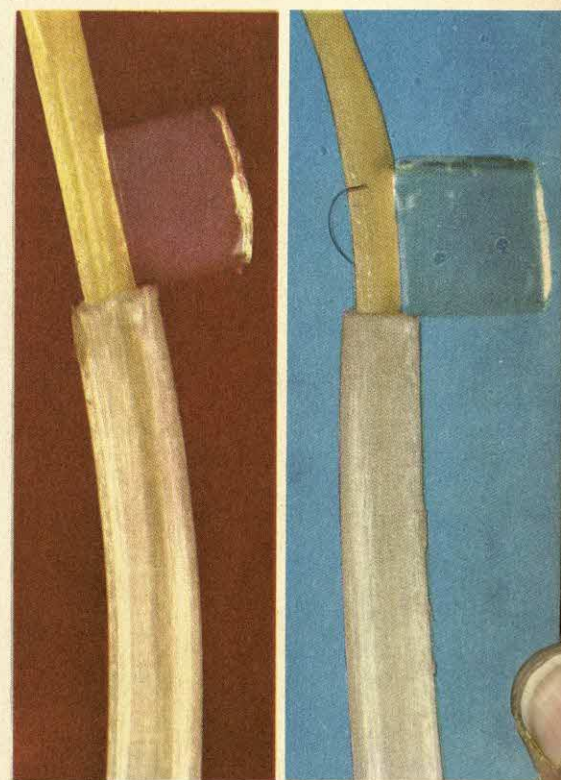
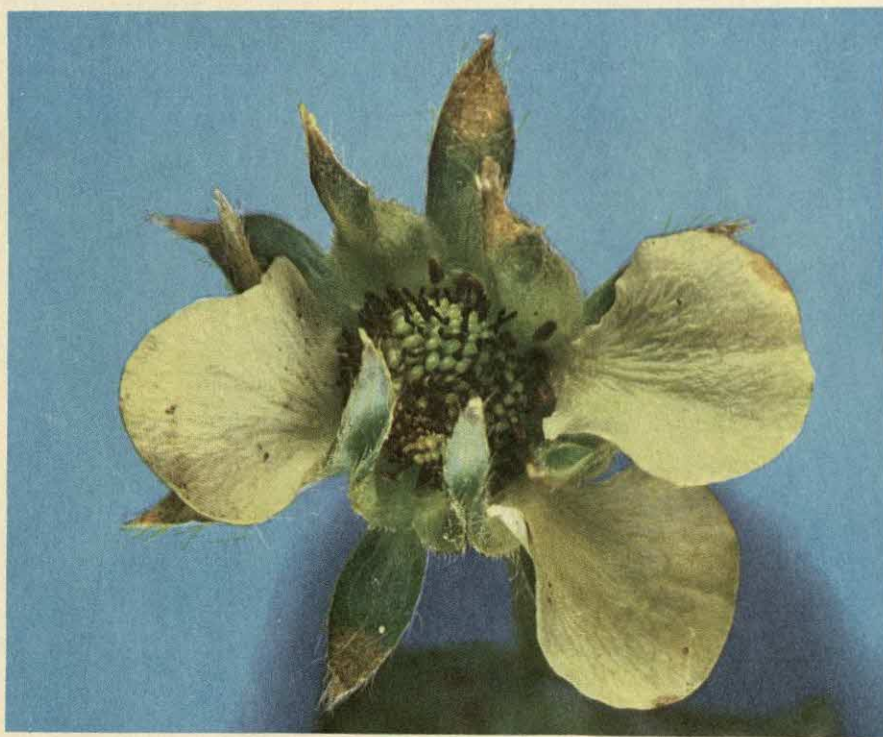


Fig. 3. A cube of agar gel containing an auxin placed on one side of the coleoptile of an etiolated oat plant (left) causes a more rapid growth of the cells underneath it than occurs on the opposite side. (Preparation by Nitsch. Photo Lod).

Fig. 4. (a) A strawberry flower (variety 'Surprise des Halles'). In the centre the pistils, with yellow stigmata at the tips, surrounded by the stamens which produce yellow pollen grains.



The Strawberry—a result of regulation by hormones



(b) In the absence of any fertilization, the styles go brown and neither the pistils nor the receptacle develop; there will be no strawberry.

(c) After fertilization the pistil enlarges into an achene, which then induces the fleshy receptacle around it to grow. The other pistils, which have not been pollinated, do not exert any inductive effect.

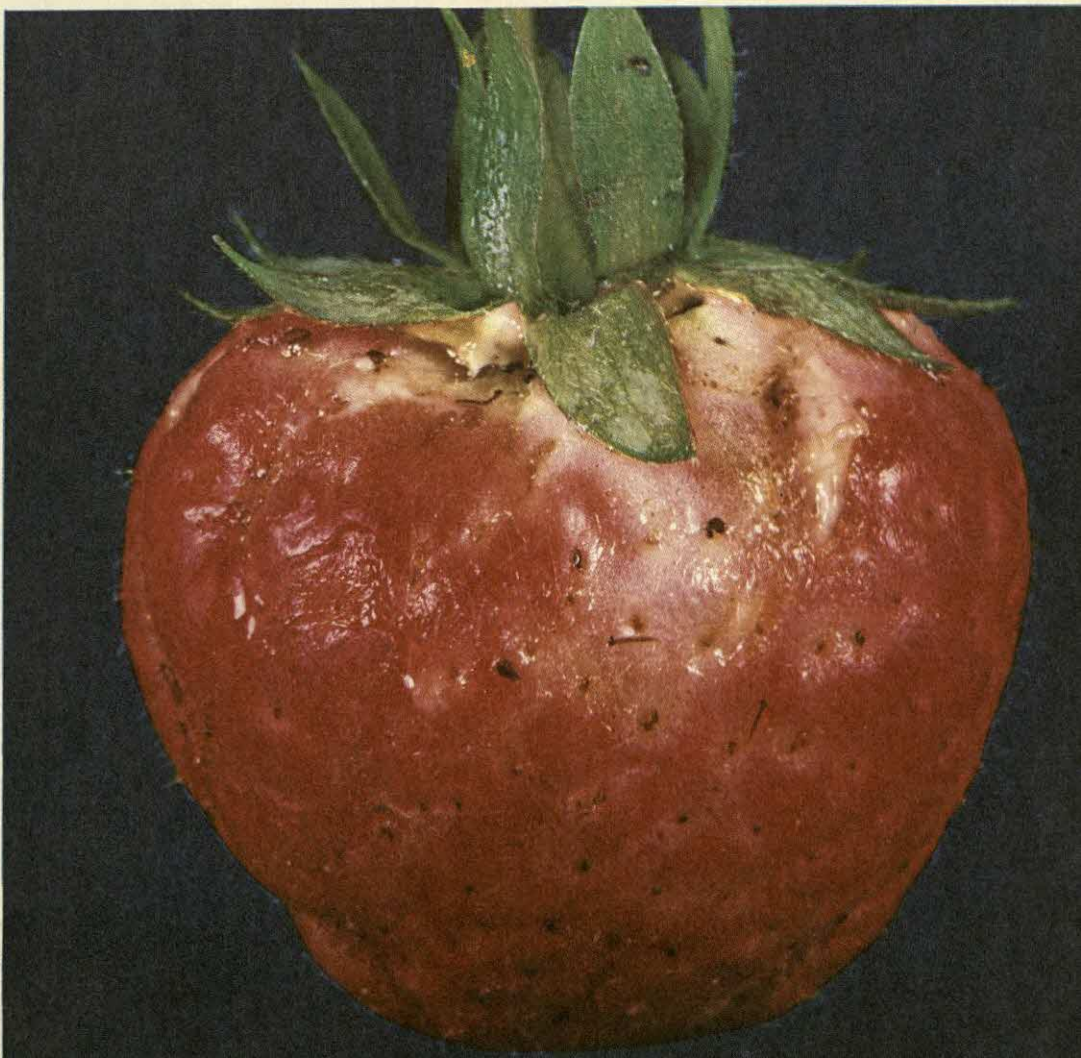


(e) In sum the strawberry is the integrated product of the zones of proliferation of the receptacle, induced by neighbouring achenes.

(d) Each developing achene induces the fleshy receptacle around it to grow.



(f) The young achenes of the strawberry can be removed and their action replaced by that of auxins incorporated in an ointment. A seedless fruit then develops normally. (Experiment by Nitsch. Photos Lod).



COMPARATIVE PROPERTIES OF THREE GROUPS OF GROWTH SUBSTANCES

AUXINS. Example, indole-3-acetic acid. Is found in immature maize weeds. Biological test, the bending of oat coleoptiles (Went).
GIBBERELLINS. Example, gibberellic acid. Found in cultures of *Gibberella fujikuroi*. Biological test, the enlargement of dwarf mutants of maize (Phinney).
KININS. Example, 6-furfurylaminopurine. Product of the decomposition of deoxyribonucleic acid. Biological test, the proliferation of cultures of the pith of tobacco plants (Skoog).

	Auxin	Gibberellin	Kinin
<i>Action on cellular elongation</i>			
(1) Stems: (a) etiolated	+++	++	#
(b) in the light	+	+++	#
(2) Petioles	★	□	#
(3) Roots	●	#	#
(4) Certain dwarf mutants	#	+++	#
<i>Action on cellular division</i>			
(1) Cambiums	+++	#	#
(2) Primary meristems of stems	#	+++	#
(3) Initiation of roots	+++	●	#
(4) Initiation of buds	●	?	+++
<i>Flowering</i>			
(1) Long-day plants (rudbeckia)	#	+++	#
(2) Short-day plants (chrysanthemum)	●	#	#
(3) Plants requiring vernalization (carrot)	#	+++	#
(4) Pineapple	+++	?	#
<i>Fruiting</i>			
(1) Parthenocarpy	+++	+++	#
(2) Ripening	+	+	#
<i>Germination of seeds</i>			
(1) Photosensitive (lettuce)	●	+++	++
(2) Needing cold (peach tree)	●	+++	?
<i>Growth of leaves</i>	a	b	c
<i>Development of buds</i>	●	++	+
<i>Detachment of fruits and leaves</i>	●	++	#
<i>Entry of water into cells</i>	+++	+	#
<i>Growth of embryos</i>	●	++	+
<i>Circulation in the plant</i>	d	e	f

- + The number of crosses indicates the strength of the stimulation.
- # No action
- ★ Epinasty
- Hyponasty
- Inhibition
- a Veins
- b Veins and mesophyll
- c Mesophyll only
- d Polarized
- e Not polarized
- f Does not circulate

Concept of the plant hormone

The properties of a hormone, in the strict sense of the word, can easily be understood from an example. Take the flower of a strawberry (fig. 4a): it consists basically of a receptacle, on which a large number of pistils are mounted, whose styles stick out like the bristles of a brush. If only one of these styles is pollinated, as it develops, part of the receptacle grows round it rather like a wart (fig. 4c). If four pistils are pollinated, four warts are obtained, and similarly, if a large number are pollinated, a more extensive growth which forms a mass of flesh will be produced, ie the strawberry (fig. 4d). Now if, with the aid of a microscope, we carefully study what happens after pollination, we shall find that all the phenomena of fertilization are limited to the pistil, and that nothing visible happens in the cells of the receptacle. All the same, the tissues of the receptacle begin to swell only after fertilization has taken place in the pistil. In fact if the young achenes, the real 'fruits' of a strawberry, are carefully removed with the point of a knife one or two weeks after flowering, the growth of the fruit ceases immediately. The mechanism by which the pistil starts the receptacle swelling is chemical. Once fertilized, the pistil rapidly fills up with growth substances, which can be extracted. These substances, like similar synthetic substances, can stimulate the growth of the young strawberry even if all the pistils are removed. In other words the fertilized pistils secrete a chemical substance which passes into the receptacle and starts its development. Such substance, which is produced by one organ and transported to another in which it starts off a physiological process, is called a hormone. Plant hormones are the messengers which an organ uses to transmit an 'order'—such as to grow, or to stop growing—to another organ. The interaction of buds by correlation, or of leaves and the production of flower buds, are other examples of hormonal action.

This definition of a hormone implies that the substance is made by the plant itself, and also that there is transport from the secreting organ to the receiving one. By knowing the chemical constitution of these hormones, industry has been able to synthesize very active compounds, which are either identical with the natural ones or very similar. These synthetic compounds are frequently called plant hormones, although the term is incorrect, because they are not made by plants. They do, however, come within the large

Fig. 5. Seven indolic compounds of the auxin group have formed coloured derivatives with Gordon and Weber's perchloride of iron reagent. From bottom to top: indole-3-acetylaspatic acid, present in the tomato (mauve); tryptophane (yellow); indole-3-acetic acid, one of the natural auxins (purple); indole-3-butyric acid (yellow); indole-3-acetic acid amide (pink); indole-3-acetic acid nitrile (violet); indole-3-acetic acid ethyl ester (brownish-red). (Experiment by Nitsch. Photo Lod).

group of chemical regulators of growth.

At present the number of known substances, both natural and synthetic, which influence plant growth, increases continuously. Their chemical structure varies a great deal, so that they cannot be classified according to their chemical constitution, but only according to their physiological effect. A group of compounds can often be characterized by a combination of physiological reactions, rather than by one alone. Thus both auxins and gibberellins stimulate the growth of the first internodes of the oat; but gibberellins have other properties which clearly differentiate them from auxins.

The table on page 86 summarizes the properties of the three principal groups of growth substances: the auxins, the gibberellins and the kinins. They are all organic compounds active in very great dilutions (from $10^{-8}M$).

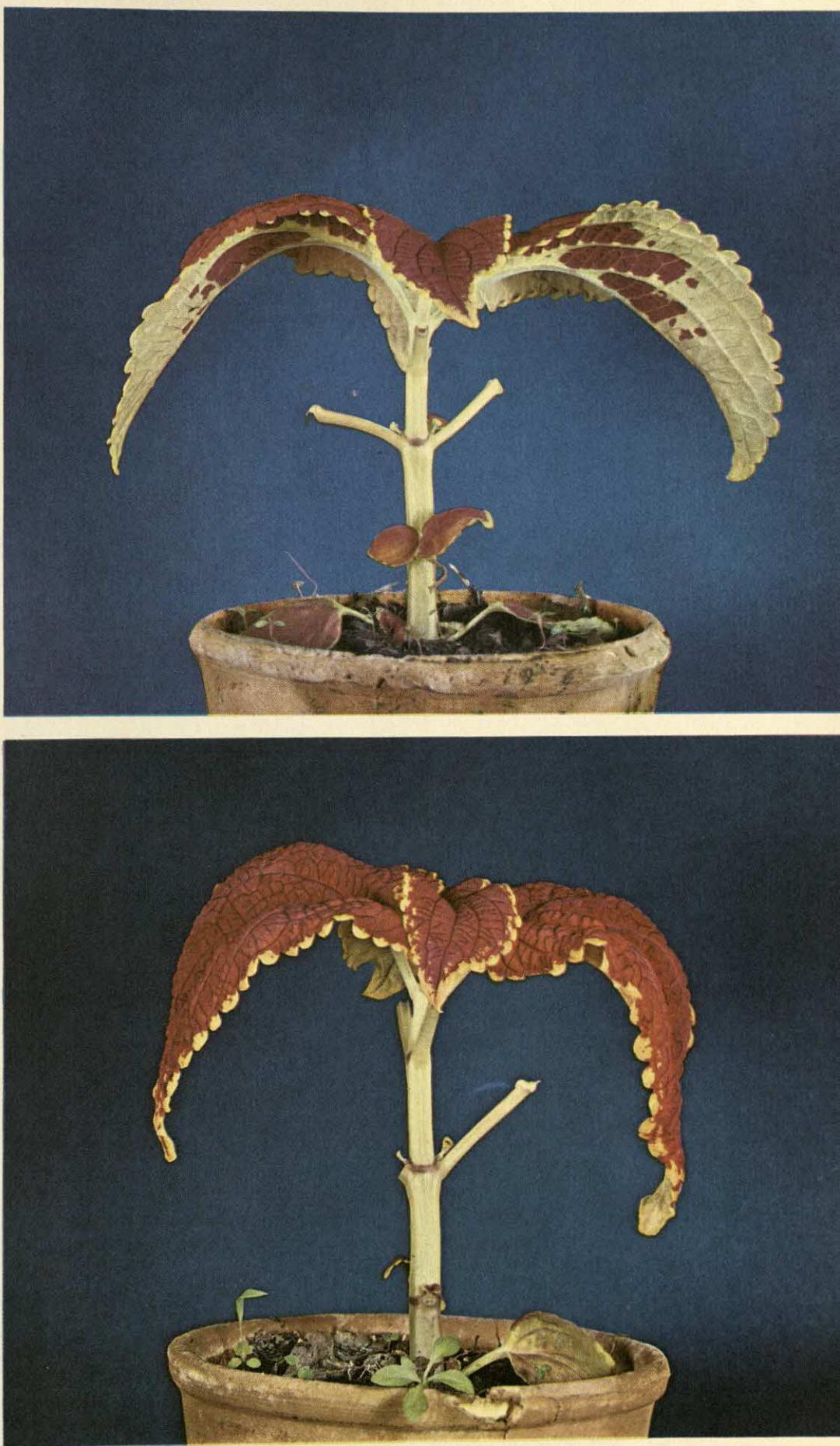
Auxins: the substances found to be active in tests such as the one developed by Went are called auxins; they form a very heterogeneous group chemically, including derivatives of benzoic, indolic, cinnamic and naphthylacetic acids. In general the molecule of an auxin consists of a non-saturated cyclic nucleus to which is attached an aliphatic side-chain with a terminal acid group.

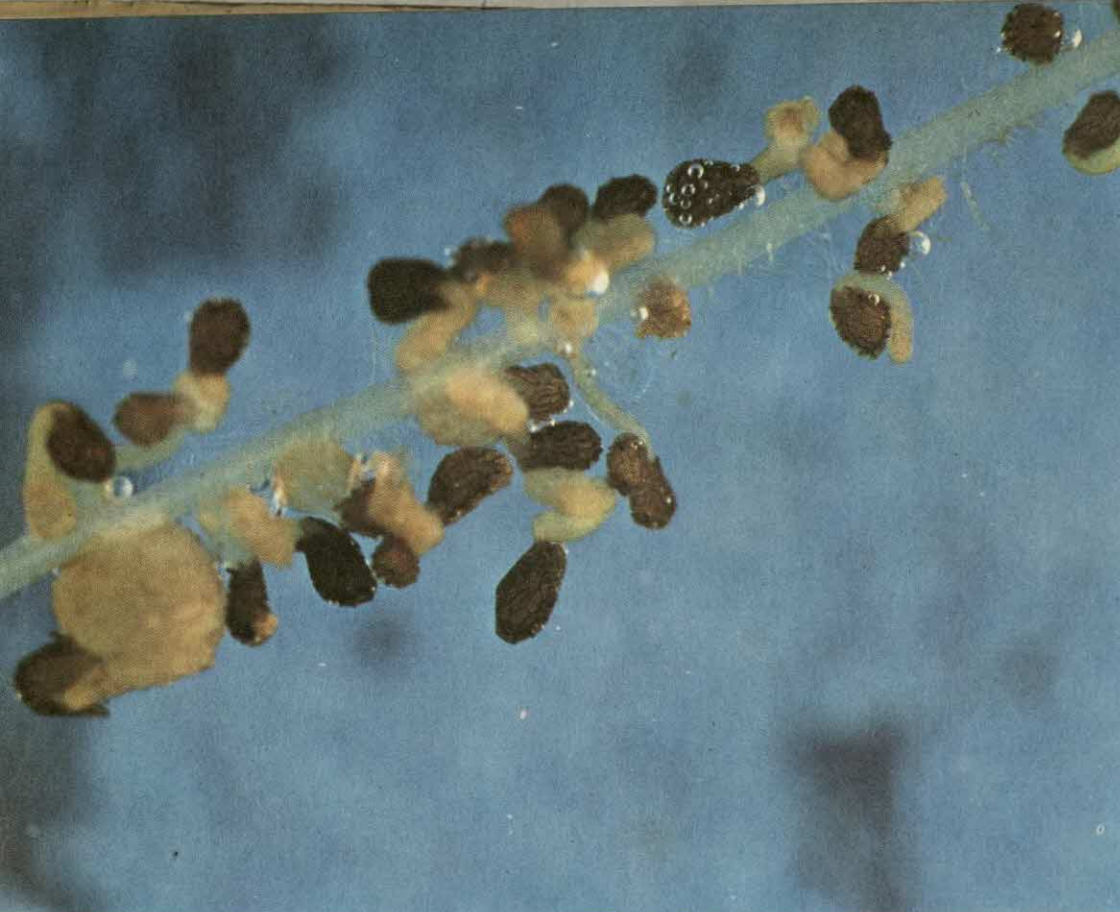
Gibberellins: unlike the auxins the constitution of all gibberellins at present known is very similar. The centre of the molecule is formed by the fluorene nucleus. Most gibberellins (A_1 , A_2 , A_3 , A_4 , A_7 , A_9) have been extracted from cultures of *Gibberella fujikuroi*. Four of them (A_1 , A_5 , A_6 , A_8) have been found in the immature seeds of *Phaseolus multiflorus* (see figs. 2, 8; and table on page 86).

Kinins: this name was given by Skoog and his colleagues to the substances which primarily regulate cell divisions. They are derivatives of purine bases which would seem to take part in the metabolism of nucleic acids. Up to now the only chemically defined kinins have been obtained by the decomposition of deoxyribonucleic acid, or by synthesis. The best known is kinetin (6-furfurylamino-purine). The physiological properties of kinins are shown in the table on page 86.

Besides these three groups of compounds,

Fig. 6. Auxins prevent leaves, flowers and fruits from detaching themselves from their stalks. If the leaf-limbs of *Coleus blumei* are cut off, petioles (leaf stalks) fall off a few days afterwards. Above: the cut ends of the leaf stalks have been covered with an ointment containing either water (left) or an auxin (right). Below: after a week the petiole treated with water has fallen off, and the other is still in place. (Experiment by Nitsch. Photo Lod).





(¹) The work of Chabrolin (1939) brought out several important facts. On a plate of glass he placed two discs of wet filter paper uniformly covered with the fine seeds of *Orobanche*. He put the whole thing in an earth-filled pot, with the glass plate at an angle to prevent the water stagnating. Under these conditions none of the seeds germinated. He then planted a broad-bean seed on the surface of the earth; in the course of germination, the root of the bean grew down and came up against the filter papers and glass. It then had to bend and grow along the surface of the filter paper. After a few days the pot was emptied carefully, so as not to disturb the filter papers. On them, as on an x-ray plate, could be seen the track of the root and the rootlets marked by the lines of germinating seeds of the *Orobanche*. The proximity of the broad-bean roots had been sufficient to set off the germination of the seeds. The effect was produced through the thickness of the filter paper, which suggests diffusion of a chemical substance. Chabrolin established this by showing that aqueous extracts of young roots stimulated the germination of *Orobanche*.

there are other substances regulating growth, but whose chemical composition still remains to be found. The practical difficulties are very considerable. The organs richest in growth substances contain something like 0.1 mg per kilogram of fresh tissue. That is to say that one has to throw away 99.99999 per cent of the plant material in order to obtain the one ten-millionth part that is interesting. It is rather like searching for a needle in a haystack. A few examples of these substances follow:

Factors influencing the germination of parasitic plants: the seeds of parasitic plants are often provided with mechanisms which make their germination dependent on the proximity of the host plant—without which they could not last. Such is the case with one of the *orobanche* family (*Orobanche speciosa*) which infests the broad-bean fields of North Africa¹ (fig. 7).

Flowering factors: most chrysanthemums do not flower while there are 15 hours or more of daylight; they need the short days in order to flower. Nevertheless, once they have started to produce flowers, the days can be lengthened without interrupting the formation of flower buds. Under these conditions they are said to be 'induced to flower'. If two chrysanthemums, one of which has been induced, are grafted together and the plant is given long hours of daylight, the induced stem will make

the non-induced one flower. Biologists think that a material element passes from one plant to the other and they have even given this hypothetical substance a name: 'florigen'.

In spite of the efforts of several laboratories, the chemical constitution of florigens is not yet known for certain, although several research workers have obtained substances that produce flowering, out of plants that have been induced (fig. 1). The formation of male and female sexual organs on the prothalli of ferns is also controlled by chemical factors secreted by the plants, as Naf has shown.

Inhibitors: inhibitors are important to plants. They prevent seeds from germinating or buds from opening when conditions are unfavourable. From a chemical point of view, inhibitors are legion. Some of them seem to be simple enough compounds, like coumarin and various phenolic acids, but the identity of many of them remains unknown.

This outline of the substances regulating plant development should have given some idea of the large number of compounds that exist and of the difficulties of studying them. Although it is still a small one, the list of substances already identified would give great pleasure to the great German physiologist, Sachs, who predicted as early as 1880 that substances must exist in plants to control specifically the development of roots, stems, leaves and flowers. In fact the compounds which have been discovered often have multiple actions, so that the formation of one organ is a result of the interaction of several factors simultaneously.

The chemical industry has already taken one aspect of the question into its hands. Throughout the world chemists are synthesizing compounds, and their effects as plant regulators are tested. In this way was originated 2,4-D (2,4-dichlorophenoxyacetic acid), a very active auxin usually employed in high doses as a selective weed-killer, 1-naphthylacetic acid, 2,3,5-tri-iodobenzoic acid and a multitude of other compounds, one of which, CCC (chlorocholine chloride), has the reverse effect of gibberellins, and turns climbing plants into dwarfs. Since 1952 industry in the United States alone has produced some fourteen million kilograms (thirty million pounds) of some of these products, which are, however, employed only in infinitesimal doses—a striking example of a transfer from the university laboratory to chemical industry.

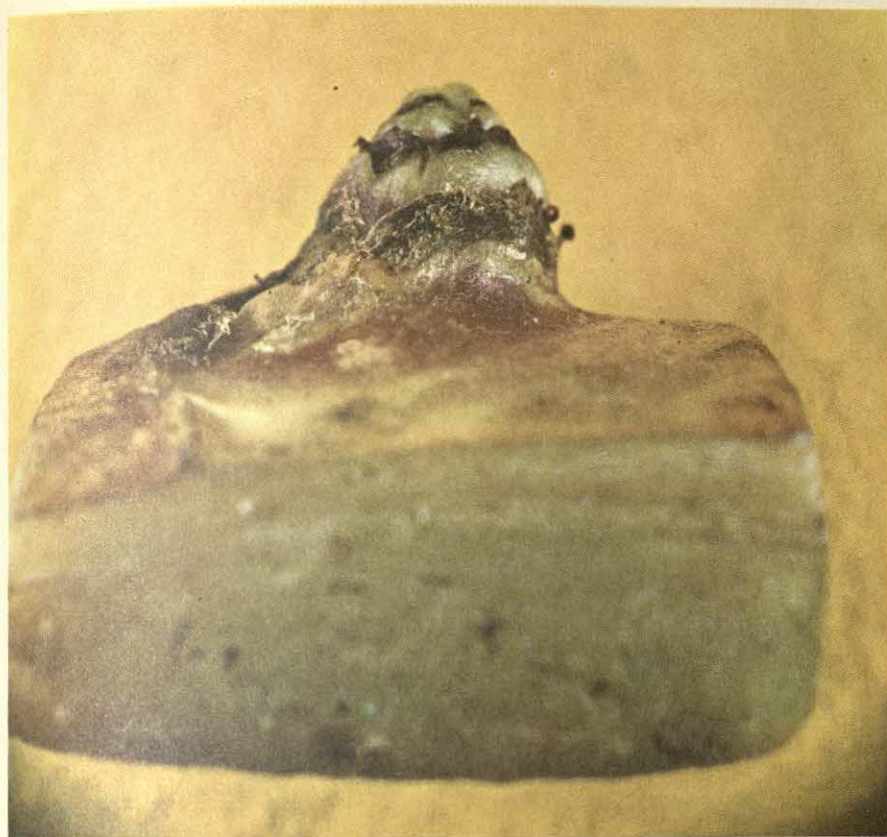


Fig. 7 (opposite page). Germination of Orobanche seeds near a root of hemp. In the course of germination a mass of cells develops which spreads out on the surface of the root. (Photo Lod).

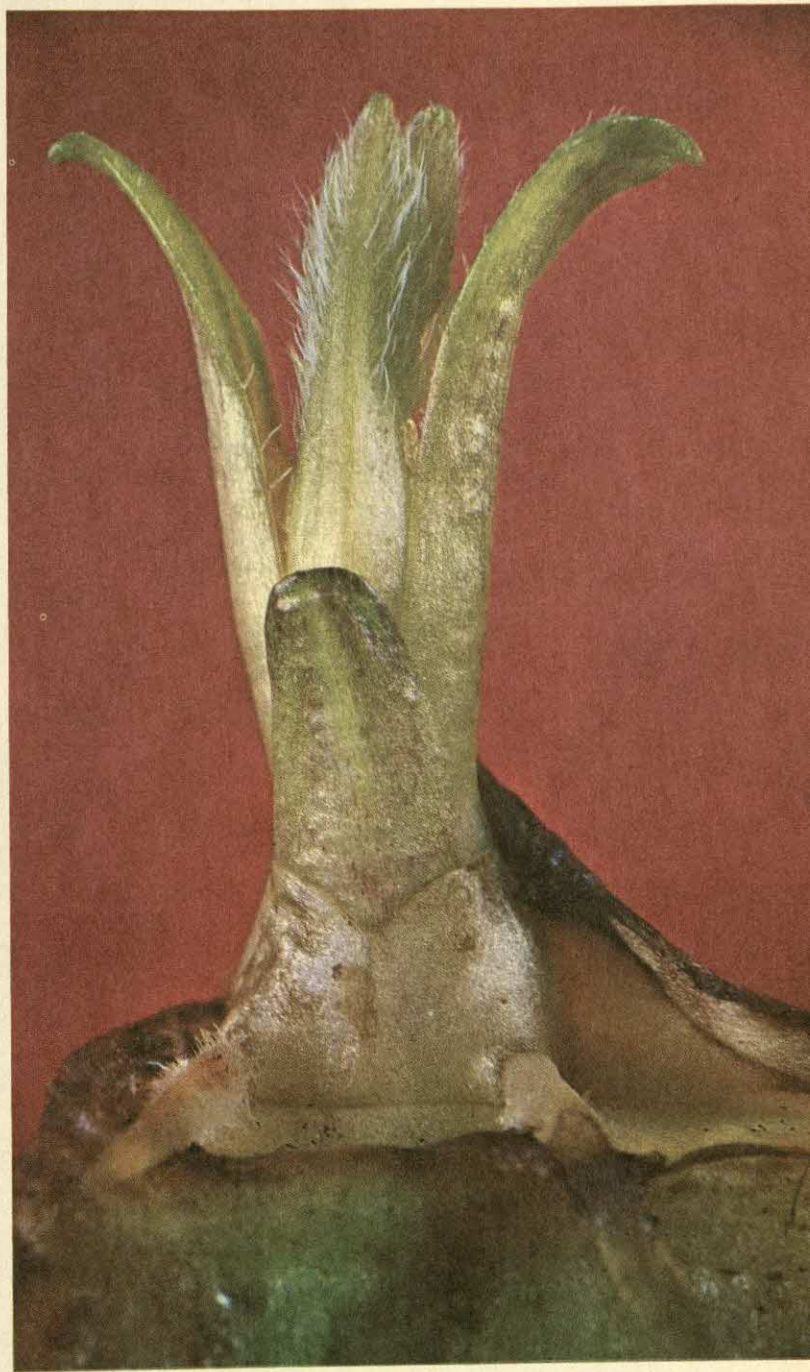
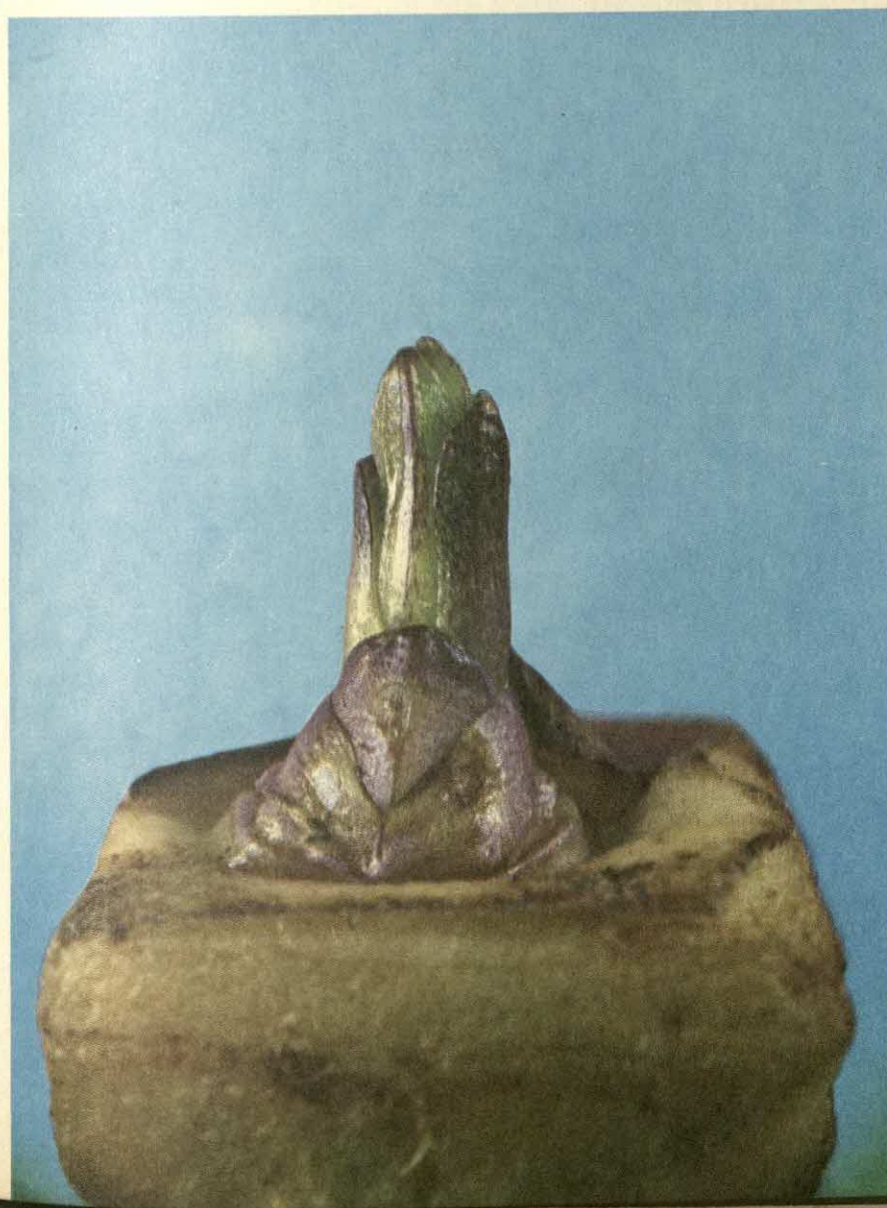
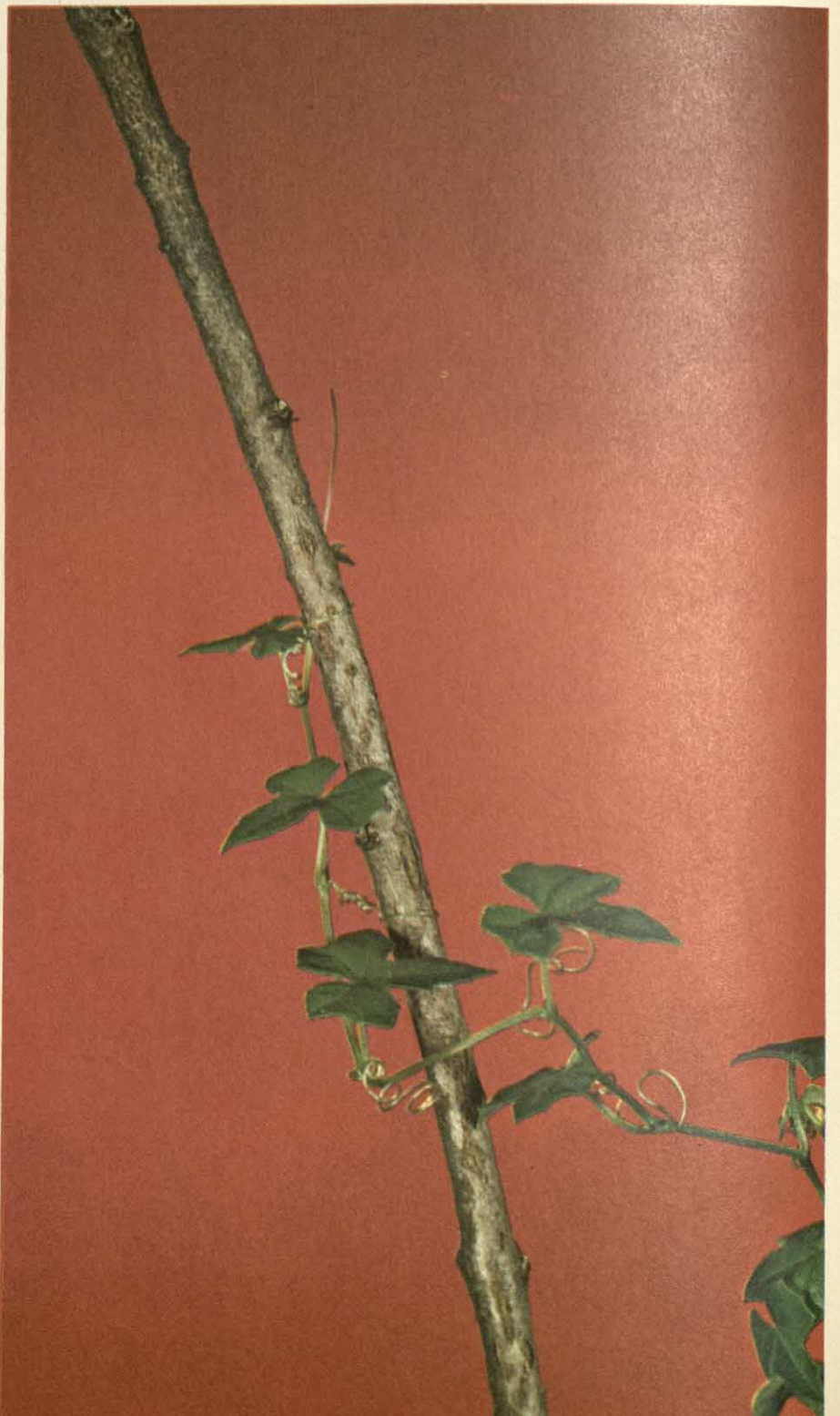


Fig. 8. Auxins and gibberellins have a different action on buds. An isolated bud from a tuber of Jerusalem artichoke placed in water develops normally (blue background). Another treated with an auxin, indole-3-acetic acid, is strongly inhibited (yellow background). Gibberellic acid, on the contrary, accelerates growth (red background). (Experiment by Nitsch. Photo Lod).



*Fig. 1. Plants are supposed to be immobile, and yet the following examples show that this is not axiomatic. At the side, from top to bottom, a tendril of *Melothria pervaga*, a member of the gourd family, meets a branch, attaches itself to it and winds itself round it like a spring. Below, the result: the tendril is firmly entwined and has pulled the stem close to the support. (Preparation by Nitsch. Photo Lod).*



Time and movement in plants

Lucien BAILLAUD

Plants exist both in space and in time. Internal and external factors regulate their dimensions, their shape and their position; and there are other factors determining the development of phenomena. Some particulars of the time sequence will be given first.

Sometimes internal factors are the most important, for instance, rapid rhythms with a cycle of a few minutes or a few hours, like the rhythm of contraction of certain cellular elements, or tendrils which twine round their supports (figs. 1 and 2). On a very different time scale many species of agave and bamboo flower and die at strictly determined ages, for example, *Fourcroya longaeva* dies at the age of 400 years and *Agava cantala* at about ten years; the course of their lives is almost constant, quite different from seasonal rhythms.

Environmental rhythms often have a marked effect on the development of physiological rhythms. The alternation of high and low tide, the seasons, day and night, produce wide fluctuations of temperature, illumination, humidity and aeration, which have their effect on organisms. These fluctuations in environmental conditions can leave their mark on plants. It is well known that the age of a tree-trunk can be determined by counting the rings in the wood, a mistletoe branch by the number of nodes, or a fir tree by the layers of branches. In these cases it is a question of years, but in others even days leave their mark; for instance, cotton fibres and starch grains are formed of concentric layers added to daily. But environmental fluctuations have direct effect on plant physiology. During the course of the day they are demonstrated by pheno-

mena related to the type described by Linnaeus as 'Flora's clock,'¹ and during the year by the succession of germination, flowering, fruiting, and so on. If the organism is isolated from the rhythms of its environment, the corresponding biological rhythms do not, as a rule, stop immediately.

Biological clocks

Let us consider daily rhythm. In its natural surroundings the French bean spreads out its leaves by day and folds them by night. If it is submitted to constant illumination from a given time, it continues to fold its leaves each evening and extend them in the morning. The mechanism of this rhythm has given rise to many experiments and discussions, for instance the work of Pfeffer and Bünning. An attempt was made to find unknown external factors which might be directing the rhythm, but this proved fruitless; the rhythm persists somehow in the leaf itself. In any case the period is not strictly twenty-four hours, and it is not quite the same from one variety of bean to another. This persistent rhythm seems to be due to an internal phenomenon,² with a set periodicity for the particular plant, a sort of 'biological clock'. If the bean is cultivated under constant illumination from its germination, its leaves, although they are not entirely motionless, do not have a daily rhythm. But if it is kept in the dark continuously from germination, and is then put into the light, this is enough to make the leaves move from the folded 'sleeping' position to the spread-out one. Furthermore, they subsequently fold and open normally in a period of

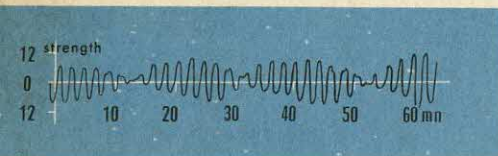


Fig. 2. Rhythmic variations in the strength of movement of a fragment of protoplasm (plasmodium of *Physarum polycephalum*). The strength is expressed in conventional units. The curve expresses the interaction of several periodic phenomena which are situated in the protoplasm. (After N. Kamiya).

(1) Two hundred years ago Linnaeus laid down the principle of 'Flora's clock' by which one can tell the time by observing the opening or closing of certain flowers. It seems as if this 'clock' depended directly on solar time.

(2) If this daily rhythm persists in plants which are kept from the normal alternation of day and night, it seems more probable that 'Flora's clock' has an internal mechanism—a 'biological clock'. The term used is deliberately anthropomorphic, but the comparison is useful. Thus, the 'biological clock' of the leaves of the French bean has an internal mechanism with a definite cycle, but it cannot start on its own. It does start up when the plant is transferred from darkness to light. In its natural surroundings, daily sunrise winds it up and also sets it to the correct time.

(3) When a plant behaves differently under different lengths of daily illumination (photo-periodic reactions), it seems as if it has a mechanism which can 'measure' the length of illumination. It has been found in some cases that this 'measuring' is connected with the internal periodicity of leaf movement.

about twenty-four hours (figs. 4 and 5). The period of this perpetual rhythm is, therefore, not imposed on the plant by the alternation of day and night; it has an internal origin, generally. Rhythms dependent on the alternation of day and night are observed not only in the movements of the leaves and flowers of innumerable plants, but also in such phenomena as the release of perfume by flowers, the rising of the sap, and growth. Many of these physiological rhythms can persist in the absence of daily fluctuations in environmental conditions. This internal cycle of about twenty-four hours which is so widespread, has similar characteristics in most cases.

The mechanism of 'biological clocks' is not understood at all well. According to Bünning, it is a question of the continuous formation of a factor concerned with the production of energy, which energy is periodically used up whenever a certain quantity has accumulated. The phases of accumulation ('tension'), and consumption ('relaxation'), in this cycle are bound up with the variations of

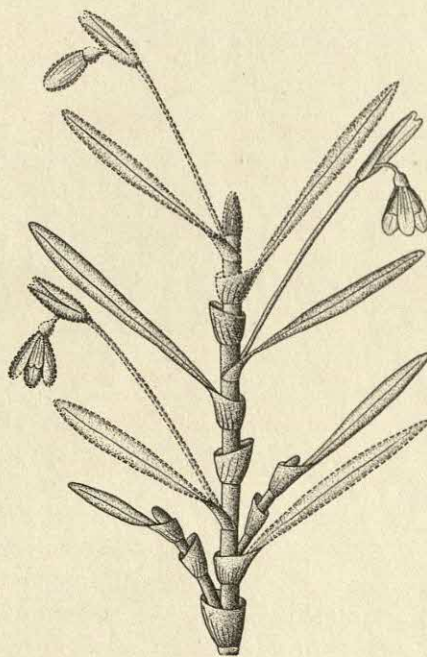


Fig. 3. A rhythm with annual periodicity. This diagram shows theoretically how the stem, leaves and flowers of the snowdrop develop in the course of several years. Each year a scale surrounding the stem, a leaf with a broad base, and a leaf with a narrow base are formed. The flower develops in the axil of the latter leaf. The stem is actually very short, so as to form a bulb with a group of leaf-bases and scales. The plant grows upwards and dies at the base so that the size remains limited. The dotted lines represent the previous year's dead organs, and those which will develop in the following year. (After Braun).

certain pigments. But what is the actual basis of this cycle? Does it take place in the nucleus, as some have supposed? Do biological clocks have similar mechanisms in all plants (and perhaps in all living organisms)? Finally, what is their role³ in adaptation to climate?

Seasonal rhythms also have their role in plant life. In regions where the seasonal differences are very marked, the plants which survive are those whose development harmonizes with the climatic rhythms. Research on the physiology of the seasons has shown that it is as if in summer the plant prepares for the winter, and as if it needed the severity of winter in order to be able to continue its development the following spring. It must be concluded that plant development is regulated both by the calendar of the actual seasons and by some sort of internal calendar (figs. 3 and 6).

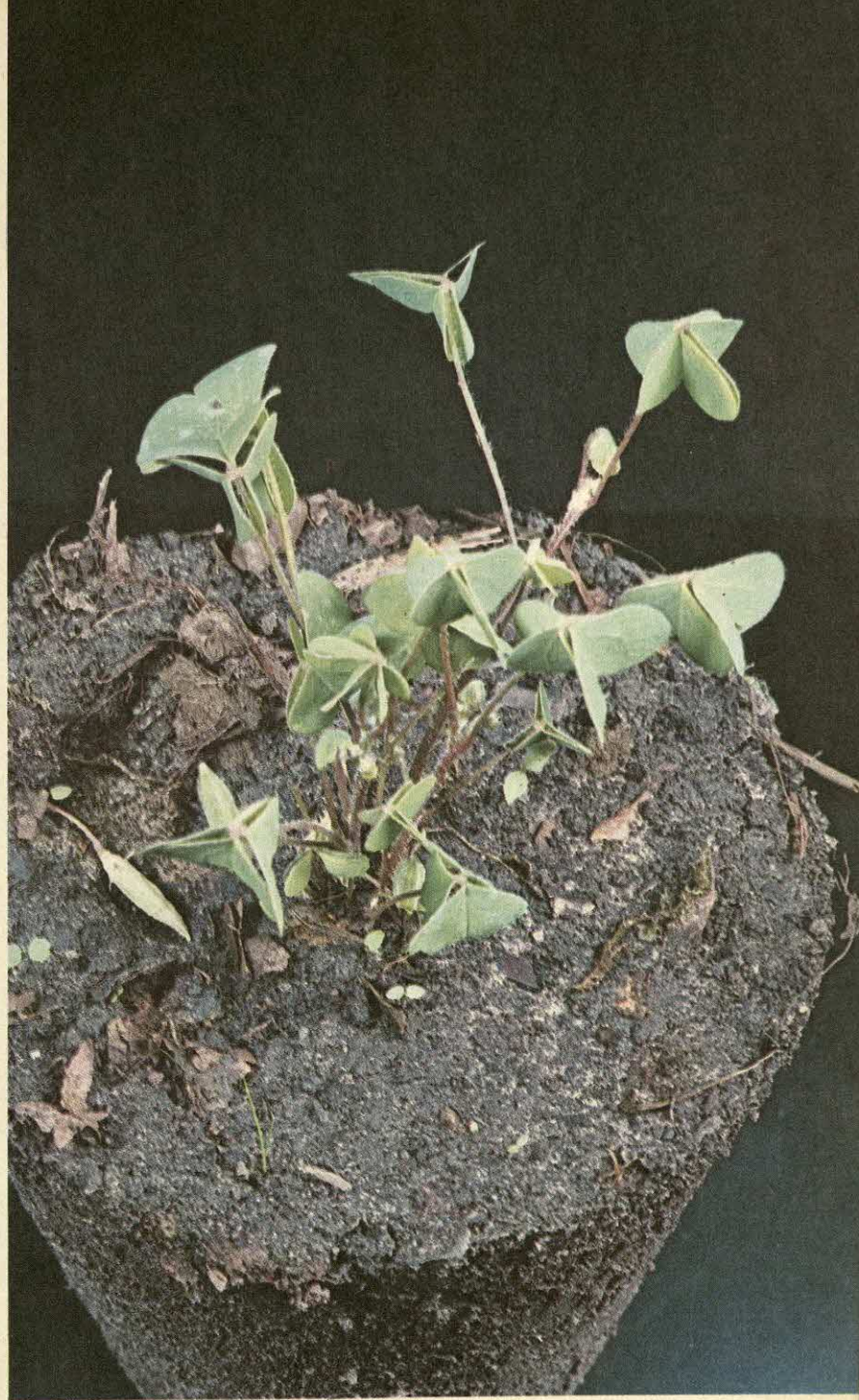
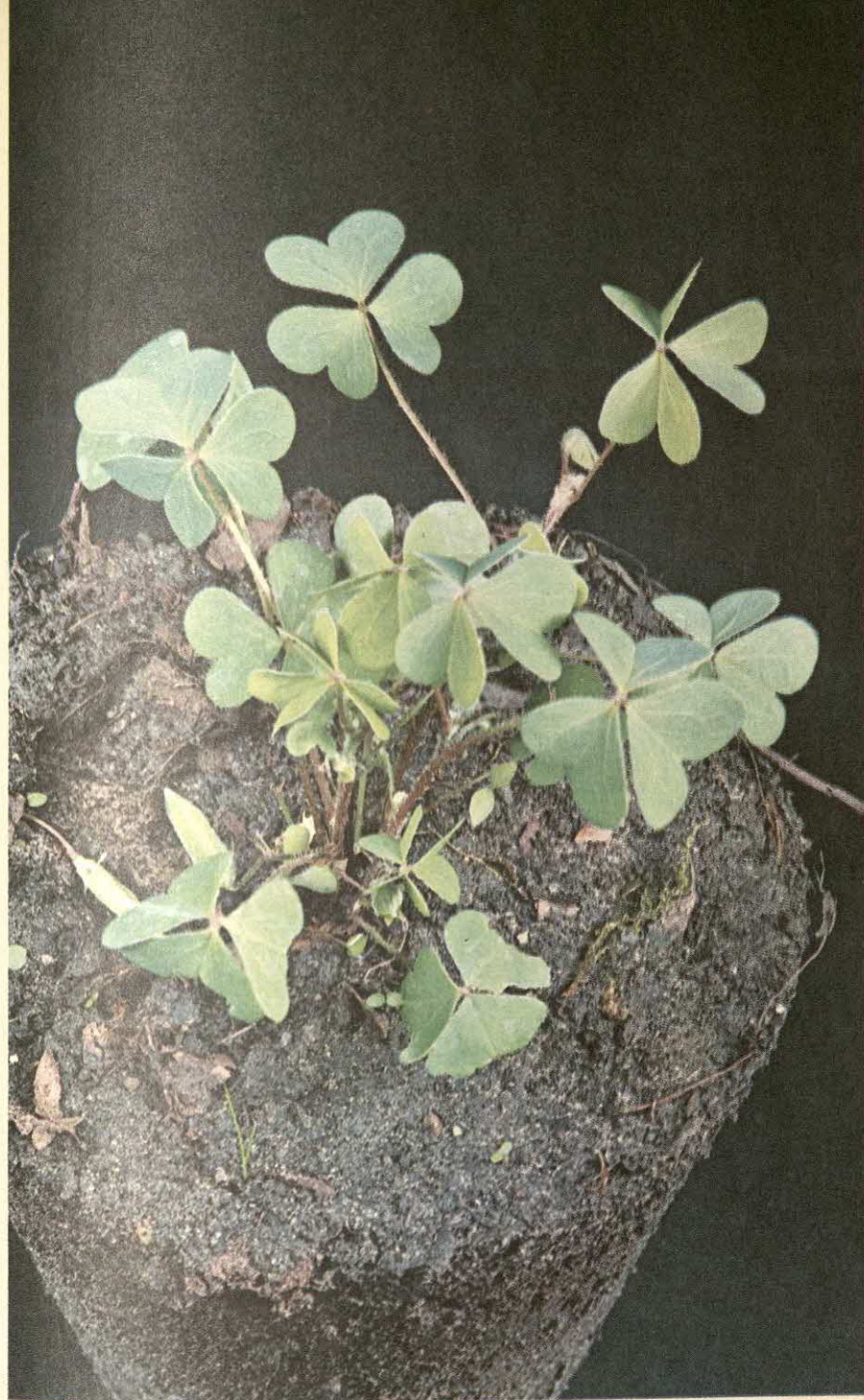
Tactisms and nastic movements

Plants also develop spatially. Certain movements are almost spontaneous: for instance, inside the cell there are rapid currents circulating; the normal growth of a stem or root makes the apex of the plant move more or less in a straight line. The stem of a climbing bean makes wide movements so as to twine itself round its support. These movements are basically regulated by internal mechanisms, which are not always easy to analyze; more is known about the movements induced from without. Stems, leaves and roots have varying degrees of sensitivity to gravity, light and humidity, which contribute in imparting the plant's characteristic aspect: the roots grow down into the earth and the stem grows upwards into the air.

On a microscopic scale, there are also movements which are really the result of stimulation, but of a different nature, for the whole organism, being free to move, displaces itself bodily. Such a movement is called a taxis. For example, unicellular algae move towards light sources, or towards regions richest in oxygen. Other micro-organisms are sensitive to the concentration of salts in the water, or to gravity. Certain parts of the cell also, like the nucleus, move under certain stimuli.

Most higher plants have a fixed position in the soil, so that normally, they cannot move, in the true sense of the word, from place to place (pollen and seeds excepted). Their movements consist of bending and these are called tropic or nastic movements.

If tulips are taken from a cool to a warm environment, their flowers open wide, and if



they are put back in the cool, they will close up again. This is typical nastic movement, but there are different types. They are brought about by outside stimuli, such as a variation of temperature or light. But a bending movement must have a definite direction, and how can a diffuse stimulus produce this? This sort of thing occurs in petals and leaves, for instance, which have two differentiated surfaces, the upper and the lower; here movements are produced by variations in the length of one or other surface. Sometimes these variations consist of successive stages of irreversible growth, but more often they are simply reversible changes in cell volume, that is to

say, they can appear in fully-grown organs.

It must be remembered that the stimulus and sometimes the intensity of nastic movements depend on environmental factors, whereas their orientation is internal. Often the endogenous twenty-four-hour cycle (fig. 4) controls nastic movements.

Tropisms

The word 'tropism' covers numerous movements which generally appear within the following conditions: a young organ, ie, with growth potential, comes under the influence of an external orientated factor, such as a light or heat source, gravity, etc., reacting with

Fig. 4. Left: the sorrel extends its leaves during the day. Right: it folds them at night. (Experiment by Nitsch. Photo Lod).



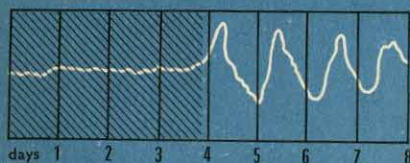


Fig. 5. A graph showing leaf movements of a French bean plant. At first, the plant is grown under uniform conditions, in continuous darkness (left-hand part of the diagram). The leaves show only slight movement. Then, the plant is placed in continuous light; the leaves rise at once, then they are lowered, raised again the next day, and so on. The simple process of transfer from darkness to light has set off a persistent rhythm with a period of about one day. (After E. Bünning).

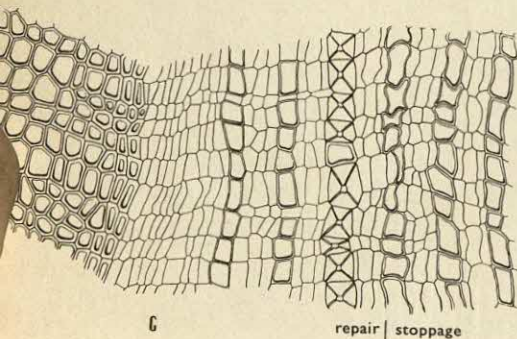


Fig. 6. Transverse section of a juniper stem. The growing zone (G) in the 'bark' is formed of flattened cells which divide actively and always in the same direction. In this zone cells are produced which line themselves up in the same direction as the medullary rays of the tree (roughly horizontal in the figure). The cells become wood, left, and bast (phloem), right. According to the season at which the wood is formed, the vessels are either large or small. This is how the annual rings are made. (After Y. Courtot).

unequal growth on the exposed and unexposed sides; it is then governed by incurvation, eg bending towards the light or drawing away from it. All tropisms set physiological problems which can be presented schematically in the same way. These problems are concerned with the nature of the active external factor, its perception, the transmission of the stimulus and the reaction to it.

Phototropism, a curving movement orientated by light, is probably the tropism about which most is known. For instance, a typical case is the aerial part of a very young oat plant a few days after germination. This is a thin, smooth organ with a very simple structure. When it is lit from one side the base bends and it curves towards the light to an extent determined by the intensity of the stimulus. The non-illuminated side grows longer than the illuminated one, whilst the apex of the plant remains more or less straight, and seems to be passive.

Darwin's ingenious experiments showed that in fact it is the tip which perceives the stimulus; it is sensitive to light but it does not react itself. The stimulus is conducted through the tissues towards the base, the area where the reaction, bending, occurs. We now know that the tip of the oat plant normally produces growth hormones, 'auxins', which move into regions lower down the stem, with the result that growth then starts there. If the tip is lit from one side, less auxin is freed on the illuminated side than on the other.

The phenomenon of phototropism is still not fully explained, since we do not know, for example, the mechanism by which light is perceived; perhaps it is the action of some sensitive coloured substance. Nor do we know how it is that lighting from one side produces an unequal distribution of auxin.

Thus the initiation, orientation and intensity of tropic movements are caused by external agents.

Carnivorous plants have various kinds of trap which capture small insects and digest them. In most cases these consist of sensitive leaves which react to contact or to shock by folding together. The round-leaved sundew is a small marsh plant. Its leaves are little more than one centimetre in diameter, and carry movable grasping tentacles formed by a long filament with a small glandular head, which is sensitive. If this is removed the tentacle no longer reacts. The membranes of the superficial cells on this glandular head are very thin in places, so that when the insect touches the head it provokes an excitation inside the cells.

This excitation must be strong enough or often enough repeated to produce a visible effect. It is transmitted towards the base of the tentacle, where it produces unequal swelling of the cells so that the tentacle bends and bears down on its prey.

Sensitivity among plants

Taxis, nastic movements and tropisms are not passive but active responses to stimuli from the external environment, ie, the plant has to be excited to action. The essential problem is therefore plant sensitivity. It is a question of irritability, which is a well-known property of living matter, but less widespread in plants than in animals.

One of the best examples of this is the sensitive plant, mimosa. This plant has composite leaves, which are jointed. The petiole is inserted in the stem, and it carries many branches, each covered with a number of leaflets normally spread out. If these terminal leaflets are touched, they spring up abruptly; this action then spreads to other leaflets nearby at a speed of several millimetres per second, in the direction of the petiole. If the stimulus is intense enough it also has effect on the petiole, and may spread to nearby leaves. The reaction of each joint and the springing upright of each leaflet, consisting of a rapid contraction of one part of the tissue of the joint, are completed in a few seconds at the most. The mechanism is thought to have something to do with the movement of an active substance, but let us limit ourselves to the character of the irritation itself and its first effects.

If the shock is too slight, nothing happens, so that a certain minimum of intensity (a 'threshold') is necessary. But once the threshold is reached, provided that the other conditions are favourable, the reaction of the leaflet is complete, that is to say that it is 'all or none'. The reaction begins very soon after the stimulus, and the springing upright of the leaflet is completed in a few seconds. The return movement begins almost at once and after fifteen or thirty minutes, the leaf is back in its normal position. From the moment the shock is administered, the leaf is insensible to further excitation, that is, it is 'refractory', even if the second excitation is stronger than the first. This refractory state lasts several minutes, even after the returning movement begins. Irritability reappears little by little.

Even if plants do not have a nervous system, they do possess rudimentary mechanisms which make them sensitive and allow them to react to factors in their environments.

The climates and seasons



*Desert in
flower at
Borejo,
California
(Photo
Feininger).*

Creating an artificial climate

R. E. L. and Marie BOUILLENNE

Life on the earth's surface, whether animal or vegetable, depends on the correct functioning of leaves, whose cells contain a green pigment known as chlorophyll. Bathed in sunlight, these cells carry out the photosynthesis of sugar, fats and proteins on which the nutrition of all living beings is based. Indeed, the old maxim is still true: 'All flesh is grass.'

(1) Observation and recording of most environmental factors is not sufficient to determine their precise action because they are very variable, not only in nature but under experimental conditions.

(2) In a well-constructed phytotron, plants are completely protected from air-pollution, bacterial infection, and parasites by the filtration of the air and sterilization of nutritive solutions, soils, objects used in cultivation, clothes worn by workers, etc.

Ecological data

The principal ecological factors are the following: (1) for *soil*—structure, chemical composition, moisture and mineral salt content, temperature, etc.; (2) for *climate*—content of carbon dioxide, atmospheric humidity, velocity of wind, temperatures by day or night; (3) for *light*—its intensity, its length by day, its spectral composition; (4) for *environment*—microbiological substratum, neighbouring plant communities, etc.

Before 1939, it had been possible to determine almost completely, and with exactness, the macroconstituents and the micro-

constituents of the nutritive mineral solutions required for the growth and development of a great number of plants, but the same did not apply to many other factors. It was a question of those ecological data that are of prime importance in the physiology of plants, but for which it has not yet been possible to establish experimentation on a sufficiently controlled basis.¹ How can we prevent, for instance, the disappointing interference of natural and unforeseeable climatic fluctuations? The fact that soil-less cultivation can be carried out successfully by supplying a nutritive solution (cultivation of plants in water) and eliminating the problems caused

by variations in soil, does not provide a sufficient control over all biological phenomena that have to be explained. It was desired to have an installation which would allow us to study some of these factors, either simultaneously or separately. It was imagined what progress we should be able to make if we were assured of precise control over a plant during its lifetime.

Recent advances in thermodynamics, electronics and air-conditioning have now made it possible to plan such an installation. The first, called a phytotron, was put into use in 1949 at Pasadena, California by Professor F. W. Went.

The importance of phytotrons

Phytotrons are large installations for creating climatic conditions; they consist of a number of conditioned greenhouses and laboratories in which one can establish and reproduce at any time precise conditions of environment and keep them automatically constant or make them change, according to plan. For example, one can decide to create in two adjoining rooms (or greenhouses) an equatorial climate and one of polar type. One can also establish in both of them the same degree of light, velocity of wind and composition of air, at the same time keeping constant the temperatures proper to the two rooms. One can even induce climates which do not really exist, such as an alternation of hot nights and cold days, or multiply within twenty-four hours a sequence of hot or cold intervals; one can also bring about abrupt changes of temperature or make such changes gradual; or one can compare the effects of daylight and artificial light in identical climates.

The advantages to be gained by the skilful use of such procedures are considerable. Much information is to be obtained by observing the behaviour of plants in known and stable conditions; the evolution of their underlying reactions can be recorded in detail and the part which is due to genetic factors can be separated from that which responds to factors of environment. Furthermore, if one of these exterior factors is isolated without any change in conditions in the others, we can determine and measure such reactions as are capable of valid interpretation, and which allow us to observe the optimum level of each. Research aimed at discovering for each species what are the best conditions of germination, of growth, of flowering and seeding, are thus greatly helped and the planning of experiments is also greatly simplified because, as the pheno-

typical variability is reduced to a minimum, it is necessary to deal only with a small number of plants. Professor Went has pointed out that in the case of tomatoes he had to use series of four plants only to obtain valid conclusions.

The fact that experimental conditions and results are reproducible, enables us to do away almost entirely with the heavy task of statistics to which one is bound when it is necessary to repeat the same experiments, using a great many specimens, a great number of times. Generally, with the phytotron, we need only repeat the experiment two or three times.

The results not only give one an understanding of the basic laws of the physiology of plants, but also tell us how to treat plants which are of use to us with a view to a better yield, and to distribute their culture in the ecological media which suit them best.

Three essential requirements

The size and complexity of the fittings of a phytotron obviously depend upon the type of problems to be solved, but it is essential, in whatever country it is to be set up, that its construction should provide automatic regulation for three factors: temperature, humidity, and light.²

Although the heat control of an ordinary room may be easy, it does not follow that the same is true of greenhouses, which, in the course of a year, are exposed to variations of the seasons, days, and hours, and to rapid and often considerable changes in temperature, particularly in temperate regions.

As soon as the sun breaks through clouds, its rays enter greenhouses and their power is converted into calories. The number of calories received depends on the limpidity of the atmosphere and the inclination of the sun above the horizon. At an angle of 30° , at the seaside, we assess the amount of heat received as $40 \text{ gr cal/cm}^2/\text{per hour}$; at 60° it is increased to $70 \text{ gr cal/cm}^2/\text{h}$; at 90° it reaches $80 \text{ gr cal/cm}^2/\text{h}$ (a condition similar to that of sub-tropical areas).

In regions where the state of the sky is generally clear, heat control of greenhouses is relatively easy; but in temperate regions, where cloud-formation is irregular and the weather is changeable, it is essential to have automatic equipment which responds accurately and with great speed to exterior variations in the increase or loss of heat.

In some phytotrons, such as that at Liège, the regulation of heat is accurate to within



Fig. 1. A research student pollinating tomatoes in one of the greenhouses of the phytotron at Gif-sur-Yvette, near Paris. (Photo Lod).

(3) Automatic regulation of air-temperature and humidity, by passing the air through a conditioning tunnel, and by double glazing, with an air circulation between the frames, was used in the phytotron at Liège in 1950.



Fig. 2. The climatotron, the creation of Professor F. W. Went at the Missouri Botanic Gardens, St Louis, USA, is a new type of phytotron in which a variety of combinations of temperature and humidity has been produced in an immense dome without the help of dividing walls. In the foreground is the pool for hybrids of exotic water-lilies which have been raised at St Louis. (Photo Jack Zehrt, Lemoine Skinner Jr, St Louis).

(4) 'The extraordinary possibility of repeating experiments in the highly-controlled conditions of the phytotron makes it possible to achieve in several months, with several hundred wheat plants, results which previously required ten or twenty years of experiments, using innumerable plants in open ground'. (P. Chouard, director of the phytotron at Gif-sur-Yvette, France).

(5) For instance, recent research has revealed that *Cyamopsis tetragonoloba*, a plant of considerable importance in the mining industry, flowers profusely at a constant temperature of 30°C, but seeds very badly. If it is removed to a temperature of 26°C just when the flower-buds are formed, it flowers and seeds profusely. If it is subjected to a temperature of 20°C it does not flower. With such information at his disposal, the scientific agriculturist is obviously able to find on the map of the climate of a region, or even of a continent, the area where such-and-such a plant can be grown with success. (The result of experiments carried out at the phytotron at Liège.)

$\pm 0.5^{\circ}\text{C}$. Heat is distributed uniformly by means of a considerable stirring of air which, directly and without variation, reaches every site of experimental cultivation.

In this phytotron conditioned air is renewed about 180 times an hour and contains a certain proportion of fresh air drawn in from outside, which, having been passed through a filter and purified, is then passed to the conditioning rooms, at the same time as the inside air taken from the greenhouses and the darkened rooms.

It is interesting to record that one can even obtain temperature-control changing automatically from hour to hour. Humidity in the air can be produced by several methods: one process consists of vaporizing an aerosol of water, controlled by a hygostat adjusted to the required degree of humidity. Another method is to pass the air through a conditioning tunnel where water is sprayed at the desired temperature. If it is not to be saturated, this air is chilled to the precise degree at which it loses the correct amount of water; it will then be reheated to the required temperature. This automatic control is governed by mechanically operated valves which let hot or cold water into special pipes, as required.

The question of humidity in the atmosphere becomes complicated in countries with a cold season because of condensation occurring in the greenhouses and causing water to drip. Double glazing cures this defect, par-

ticularly if air is made to circulate between the two panes of glass.³

Man's old dream of cultivating plants without sun or soil has at last come true.

Laboratories have perfected tubular fluorescent light. In these tubes of cold light, an electric discharge is made in mercury vapour at very low pressure: 0.01 mm of Hg; the radiation given off (about 2,500 Å) is converted into visible light by fluorescent powders which cover the interior of the tube. The spectral make-up of the light emitted is the function of the composition of these powders. Thus it is possible to make the light suitable either for the total requirements of the plants or for the nature of the successive phenomena that characterize the various stages of their lives: germination, vegetative growth, flowering and fructification.

The spectral composition of the artificial light used in horticulture differs from that of tubes of ordinary light. In fact, plants do not 'see' as man does and, equally, do not use all the rays of the spectrum of the sun. It has been possible to make a graph of the photosynthetic activity of green leaves and to reconstitute an artificial light which contains the wave-lengths used by chlorophyll, in such a way that relatively weak intensities (4,000 to 10,000 lux) produced from appropriate wave-lengths, satisfy the majority of species, even plants normally growing in full sun, such as the cotton plant. In temperate regions, in a clear sky in June at the seaside, the intensity of the sun's rays is about 125,000 lux. But it is not necessary to produce a similar intensity in order to obtain sturdy plants; it is quite sufficient if a well-prepared illumination based on careful study of the spectrum is applied.

In short, phytotrons allow biologists to reveal the fundamental mechanisms of plants. Phytotrons are, and will remain, installations intended for research. A considerable amount of money is required for their construction, use, upkeep and supervision. But the results they give are of great scientific and economic importance.⁴ They enable us to discover quickly and accurately the ideal conditions which each species requires to germinate, grow, flower and fructify. If we wish to focus the techniques for obtaining maximum output in cultivated plants and for deciding on the appropriate geographical area in which to cultivate them, it is essential to have results based on science. These results are acquired under working conditions where the number of tests and tentative efforts is considerably reduced.⁵

The effects of rhythmical changes in temperature

S. J. WELLENSIEK

The relation between temperature and plant growth is a striking illustration of the great diversity in the living world.

The temperature in outer space is -273°C , whilst the temperature of the sun approaches $10,000^{\circ}\text{C}$. Only within an extremely small range of temperature is plant life—and therefore all life—possible. Bacteria can stand a temperature of -250°C for a few hours, and pollen can stand -190°C for several months, if not indefinitely. But these cases are exceptional, and *growth* does not usually start at temperatures below 5°C . Seeds and spores can sometimes put up with temperatures above 100°C . There are blue algae and diatoms in hot springs which live at around 85°C . But again these are exceptions, as growth is not usual above $30-45^{\circ}\text{C}$.

The optimum temperature for growth, that is the temperature where growth is the fastest, occurs somewhere between the minimum of 5°C and the maximum of $30-45^{\circ}\text{C}$. The minimum, optimum and maximum temperatures are called the cardinal temperatures.¹ Things would be simple if all plants had the same cardinal temperatures, but this is far from the case. Tropical plants need relatively high temperatures, plants of the temperate zone need relatively low temperatures, and sub-tropical plants are in between. The matter is further complicated by the fact that each different growth process in the plant (eg mineral intake, photosynthesis, translocation, transpiration, etc) has its own cardinal temperature.

Plants seldom grow well under constant temperature conditions. They need rhythmic or cyclic temperature changes, either daily or over longer periods; this is called 'thermoperiodicity'².

Before phytotrons were invented and the influence of temperature on relatively large plants could be studied, only small objects such as seeds and, more recently, flower bulbs, could be investigated. The germination of seeds depends directly on the temperature,

given that enough water and oxygen are available. For several species the optimum is $18^{\circ}-20^{\circ}\text{C}$, but tropical species, like musk melon, need $28^{\circ}-30^{\circ}\text{C}$, and others $10^{\circ}-15^{\circ}\text{C}$. The optimum is not necessarily constant within the species: seeds which are not ripe enough have a fairly low optimum, but the reverse is true for old seeds. Some species do not require a constant temperature, but one that changes periodically. The periods usually used in germination experiments are a relatively high temperature for 4-8 hours and a relatively low one for 16-20 hours, for instance beetroot $30^{\circ}-20^{\circ}\text{C}$, tomato $33^{\circ}-20^{\circ}\text{C}$, chicory $33^{\circ}-12^{\circ}\text{C}$. The precise values have to be determined empirically.

These cases, where the temperature is changed twice every twenty-four hours, are illustrations of daily thermoperiodicity.³

The growth of many plants even after seed germination also shows a daily thermoperiodicity. This fact has been known to horticulturists for quite a time, but convincing experimental evidence could not be obtained before F. W. Went built his phytotron at Pasadena.

The influence of temperature on the germination of seeds seems to be simple, because the effect of the temperature is direct and is not changed by any other factors, provided there is enough water and oxygen. Light is extremely important for growth and the effect of the temperature depends on the light conditions. Went has introduced the useful terms 'phototemperature'⁴ and 'nyctotemperature'⁵ to distinguish between the light-period temperature and the temperature of the dark period. It was found that tomato plants grew fastest when the nyctotemperature was lower than the phototemperature. To give one illustration from Went's data: he applied photo- and nycto-temperatures of 26.5° or 17°C in all four

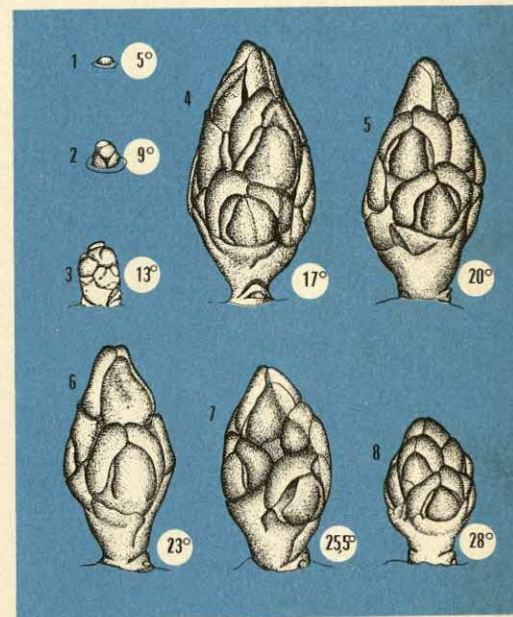


Fig. 1. Effect of temperature on the growth of the hyacinth. 8 hyacinth bulbs were exposed to constant temperatures for 3 months (the value is shown to the right of each bulb). (After Blauuw).

(1) Cardinal temperatures for plant growth: the temperatures (1) below which no growth takes place (minimum); (2) at which growth is fastest (optimum); (3) above which there is no more growth (maximum).

(2) *Thermoperiodicity (rhythmic temperature changes): the reaction of plants to changing temperatures.*

(3) *Daily thermoperiodicity: the reaction of plants to a twice-daily change of temperature, relatively high and relatively low.*

(4) *Phototemperature: the temperature during the period in which the plant is exposed to light.*

(5) *Nyctotemperature: the temperature during the period in which the plant is exposed to darkness.*

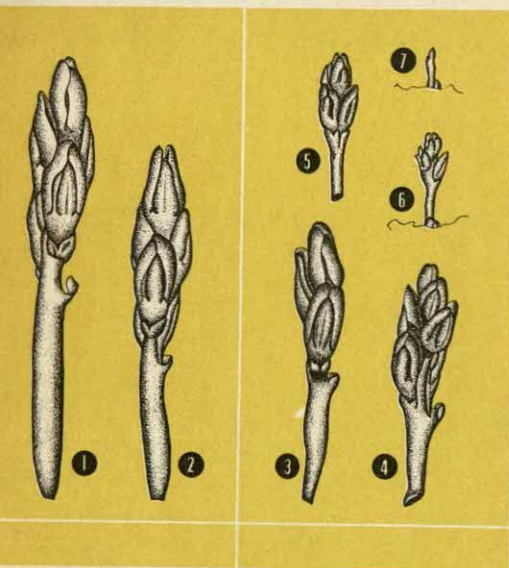


Fig. 2. Effect of temperature on the growth of the hyacinth. Left: bulbs exposed for 8 weeks to a temperature of 25.5° , and for $4\frac{1}{2}$ weeks to a temperature of about 17° . Right: bulbs exposed for $12\frac{1}{2}$ weeks to a temperature of 25.5° . (After Blauuw).

(6) *Genetic constitution consists of the inherited properties, which are mostly located in the chromosomes and which determine the reactions of a plant towards environmental factors such as temperature.*

(7) *Photosynthesis (or C-assimilation): the synthesis by the plant of organic substances from carbon dioxide and water, which occurs in daylight and with the aid of chlorophyll.*

combinations and found the average growth of the stem to be:

Temperature ($^{\circ}\text{C}$)		Rate of growth of stem (mm per day)
Day	Night	
26.5	26.5	23.1
17	17	24.3
17	26.5	24.7
26.5	17	29.3

Hence the best growth takes place with a phototemperature of 26.5°C and the much lower nyctotemperature of 17°C . However, Went established that there is no daily thermoperiodicity in very young seedlings, but that the need for lower night temperatures increases as the plants grow older. Also, when light conditions are good, thermoperiodicity is less pronounced, and when they are poor, very low nyctotemperatures are needed. The exact values of the temperatures depend on the variety and thus on the genetic constitution of the plant, and this is a further complication.

Went has tried to explain diurnal thermoperiodicity by saying that the transport of sugars in the plant needs a fairly low temperature, that is that the products of photosynthesis,⁷ which are made during the day with a high optimum temperature, are transported most quickly at night, when the temperature is low. In very young plants the distance is short and so there is less need for low temperature, but in growing plants the need increases relative to the greater distance between leaves and roots.

This explanation is not generally accepted, and other physiologists say that low nyctotemperatures decrease the respiration;⁸ and thus the substances synthesized during the day would not be entirely used up, and there would be some available for the growing plant. The history of science frequently demonstrates that there is often truth in opposing hypotheses.

Daily thermoperiodicity has been shown to exist in several other plants as well as the tomato, and yet it is not a general phenomenon. Fortanier found that the growth of the peanut is proportional to the average temperature, ie that high photo- and low nyctotemperatures have the same effect as low photo- and high nyctotemperatures. Not enough species have been investigated to produce a definite conclusion, but it does seem as if plants of the temperate zone need a daily thermoperiodicity more than do tropical plants.

Some plants flower only when they have a limited number of daylight hours (photoperiodism, or so-called short day conditions). At normal temperatures these plants do not

flower when there are many daylight hours.⁹ However, if the temperature during the long light period is very low, for instance 5°C , but normal during the short dark period, the plant often flowers. This is a case of daily thermoperiodicity, but the effect on growth is quite different from that of temperature. The explanation is that flowering is inhibited during a long light period at normal temperatures, but not at very low temperatures.

In conditions of daily thermoperiodicity, the plants are reacting to two periods of different temperatures *per day*. But there is another kind of thermoperiodicity, where a constantly low temperature of around 0°C is required for a period of several weeks to some months. The seeds of many plants, for instance, tree seeds, are in a state of 'dormancy'¹⁰ after ripening. They will germinate only after being exposed to cold in slightly moist surroundings for some months. This is called 'stratification'.¹¹ Lily seeds are interesting, because only the stem is dormant, and lily-of-the-valley seeds have both root and stem dormancy, which can only be dispelled by two consecutive stratifications.

A similar sort of thing, 'winter dormancy',¹² occurs in the buds of some plants, for instance, woody plants in temperate zones, and sometimes in herbaceous perennials, potato, gladiolus and strawberry. Buds do not form unless they have been exposed to a period of cold; if there is no such period, 'delayed foliation'¹³ occurs.

Some plants do not flower unless they have been exposed to a period of low temperature, either at the stage of seed germination, or later (eg biennials). This phenomenon, which is called 'vernalization',¹⁴ is a sort of thermoperiodicity, because low temperatures are prescribed for a period of some weeks or months. The effect of a low temperature is still unknown, but one hypothesis is that there is an inhibiting factor which is put out of action in the cold.

Thermoperiodicity in bulbs

The influence of temperature on the flowering of some bulbs is another case of seasonal thermoperiodicity.¹⁵

When tulip and hyacinth, for instance, are planted in November, the bulbs contain complete flower buds. The weather conditions prevent them from developing any more and they must wait until the spring to flower. When the bulbs are lifted after flowering, they have not yet got their new flower buds. These are formed while the bulbs are in storage, between June and November. Blauuw and his colleagues



Fig. 3. Left: hyacinth bulb showing inflorescence. Right: bulb planted in a hothouse; the stem hardly develops and the flowers open close to the bulb. Winter conditions are essential for the flower to develop normally. (Preparation by Nitsch. Photo Lod).

have been studying the flower formation since 1917 and have established that it depends directly on the temperature. Flower bulbs are fairly small and can easily be stored in a series of thermostats¹⁶ of different temperatures. By this method the influence of temperature was studied long before phytotrons were invented, and this is to the credit of Blauuw.

The effect of eleven different temperatures on the flower formation of the hyacinth bulb during 12½ weeks was the basis of an experiment. Temperatures between 1·5° and 5° were found to be too low. At 9° the flower only just began to form but at 13° it became more pronounced. From 17° to 28° complete flower formation took place, but 31° and 35° were too high. The optimum seemed to be 23°–25·5° (fig. 1). However, when the whole development from the beginning to the complete flower is studied, it is found that there are shifting optima instead of a single optimum temperature. For instance, 8 weeks at 25·5° followed by 4½ weeks at 18° gives far better results than 8+4½ weeks at 25·5° (fig. 2). Scientists have been able to make precise prescriptions for the temperatures required to induce flowering on a certain date. In practical terms this might result in flowering 'the whole year round'. By applying either very low or very high temperatures flower formation can be postponed, and this makes it possible to prepare bulbs for flowering in the southern hemisphere, where flowering should occur half a year later than in the north.

A completely new method of onion growing has been developed. Like the tulip and the hyacinth, onions are bulbs and the formation of the flowers also depends on the temperature. The optimum is rather low, around 13°, but flowers do form at between 5° and 20°, although they do not do so between 25·5°–28°. Since the purpose of vegetable onion growing is the harvesting of bulbs from plants which have not flowered, these high temperatures are applied to prevent flowers forming during a biennial cycle. In the first season small bulbs are produced from seed, which are stored at 25·5°–28° and planted out early in the following year, when they will grow only vegetatively. This results in earlier and higher yields than by any other method.

The study of thermoperiodicity offers both theoretical and practical possibilities for the future. At present we have most detailed information about seeds and bulbs, which are small, but with phytotrons it will be possible to study the temperature requirements of large plants, so that before long knowledge will increase rapidly. The system of thermoperiodicity already provides an answer to the geographical distribution of plants; their genetic constitution determines what temperatures they require and whether these should change daily or seasonally.

When more is known about the thermoperiodicity of cultivated plants, we shall be able to control their environments for optimum growth.

(8) Respiration: the breakdown of organic substances, in the presence of oxygen, into carbon dioxide and water.

(9) A 'short day' means fairly few daylight hours, say 8 or 9, and more hours of darkness. 'Long day' is the opposite.

(10) Dormancy of seeds is the condition which prevents them from germinating.

(11) Stratification consists of putting the seeds in layers alternating with moist sand, at a low temperature.

(12) Winter dormancy of buds: the condition which stops them from sprouting. It can be broken by low temperature.

(13) When winter dormant buds are not exposed to low temperatures for a long enough period, they are much retarded and irregular. The effect is a delayed foliation.

(14) Vernalization: either (1) the favourable but indirect effect of a period of low temperature upon flowering; or (2) the treatment of plants with low temperatures in order to induce flowering.

(15) Seasonal thermoperiodicity: the reaction of plants to temperatures which change over periods longer than twice a day, usually several weeks or a few months.

(16) Thermostats are boxes in which the temperature is kept constant by means of thermoregulators.

The effects of cold

Philip F. WAREING

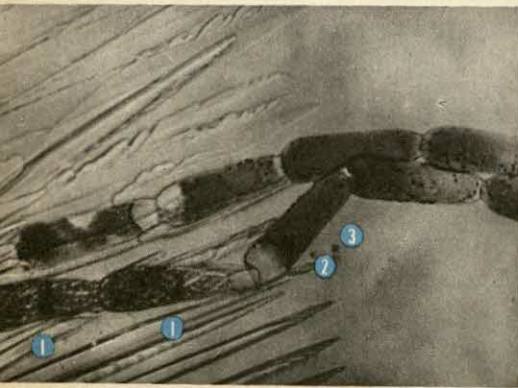


Fig. 1. Two hairs of *Tradescantia*, which have been frozen, as the ice-crystals in the water around the cells show. Ice has formed in the cells (1) which died. The formation of ice in these cells has made the water, which was not frozen, move out of the cell (2) and its vacuole, (3) has contracted. The cell which did not freeze continued to live when replaced in a normal temperature. (Photo Modli-bowska and Rogers, Jour. Exp. Bot. 1955, Oxford University Press).

In the preceding chapter we saw that the daily variation in temperature, as between day and night, has a profound effect upon the growth and development of the plant. Outside the tropics there is, of course, also an annual variation in temperature, as between winter and summer, which has an equally important effect on plant life. The low temperatures of winter affect the plant in several ways. Firstly, at cool temperatures, the metabolic and growth processes of the plant are greatly retarded, and at certain temperatures growth ceases completely.

Where freezing temperatures occur special problems arise, since plant cells normally contain large amounts of water, which is liable to freeze. Tropical plants are very easily killed by frost, but it is evident that the plants of temperate and arctic regions must have developed means for surviving; they have developed *frost-resistance*. Damage from frost can occur in at least two different ways:

- (1) If ice-crystals form within the protoplasm itself, death of the latter inevitably occurs.
- (2) During freezing there is generally a movement of water out of the cells and ice-crystals form in the intercellular spaces; this leads to dehydration of the cells, which is liable to result in their collapse with consequent mechanical damage to the protoplasm.

One of the differences between frost-tender and frost-resistant species seems to lie in the ability of the latter to withstand dehydration when ice forms outside the cell. Another characteristic of frost-resistant tissues is that their cell-sap has a high sugar-content; the result is that high osmotic forces tend to resist the withdrawal of water from the cell.

Even those species which manage to survive cold winters are not equally frost-resistant at all times of the year. During the warm period of summer their frost-resistance is low, but with the onset of cooler conditions in the autumn they become more resistant.

Dormancy

In many frost-resistant species the appearance of the plant during winter is not essentially different from that in the summer. In such species the whole plant, including the growing points, is relatively frost-resistant. Other species, however, show distinct differences between their summer and winter states. In woody plants, growth becomes completely arrested and the growing points themselves are frequently enclosed in a covering of scales, to form a *resting-bud*. The plant is then said to have entered a state of *dormancy*. It is fairly clear that the frost-resistance of dormant tissues is due to certain protoplasmic changes,

possibly of the same nature as occur during 'hardening'.

The protective function of the bud-scales is probably concerned with the reduction of water-loss. Under frosty conditions, especially when accompanied by wind, the plant continues to lose water, but is unable to take up replacement supplies if the soil is frozen. There is thus a considerable danger of damage from drought under winter conditions, but the water-loss is reduced by the enclosure of the growing points within a covering of bud-scales.

The danger of winter-drought seems not only to have influenced the evolution of woody plants, but also to have had a profound effect on the form of many other types of plant. Thus, we find many species which grow near the ground (rosette plants, cushion plants, creeping plants, etc) are covered by snow, which reduces the rate of water-loss. Others have upright shoots but these die down to soil level in the autumn and the buds of the new shoots remain partly or completely buried in the soil. Many plants *during* winter are entirely below ground, as bulbs, corms and rhizomes; although such organs will be partly insulated against frost, they will also be protected against drying when the soil does become frozen to some depth.

Whereas perennial plants have developed special organs which resist the unfavourable conditions of winter, annual plants have pursued yet another course—they frequently survive the winter in the form of seeds. The seeds of many annual plants, particularly of the common weeds of arable land, germinate almost immediately they are shed if conditions of temperature and moisture are favourable. But the seed of many other plants does not germinate immediately (or only a proportion of the seeds do so) and the seed remains in the soil until conditions become favourable for germination in the following spring. Ultimately the resistant coat becomes eroded by the activities of micro-organisms and the seed then becomes capable of taking in water, so that it can now germinate.

In discussing the subject of dormancy, it is important to make a distinction between 'imposed' and 'spontaneous' dormancy (or 'rest'). Now many seeds, such as those of apple and peach, are in a state of spontaneous dormancy when first shed in the autumn, and they fail to grow when they reach the soil, even if conditions of water and temperature are quite favourable for growth. Nevertheless, these same seeds readily germinate in the

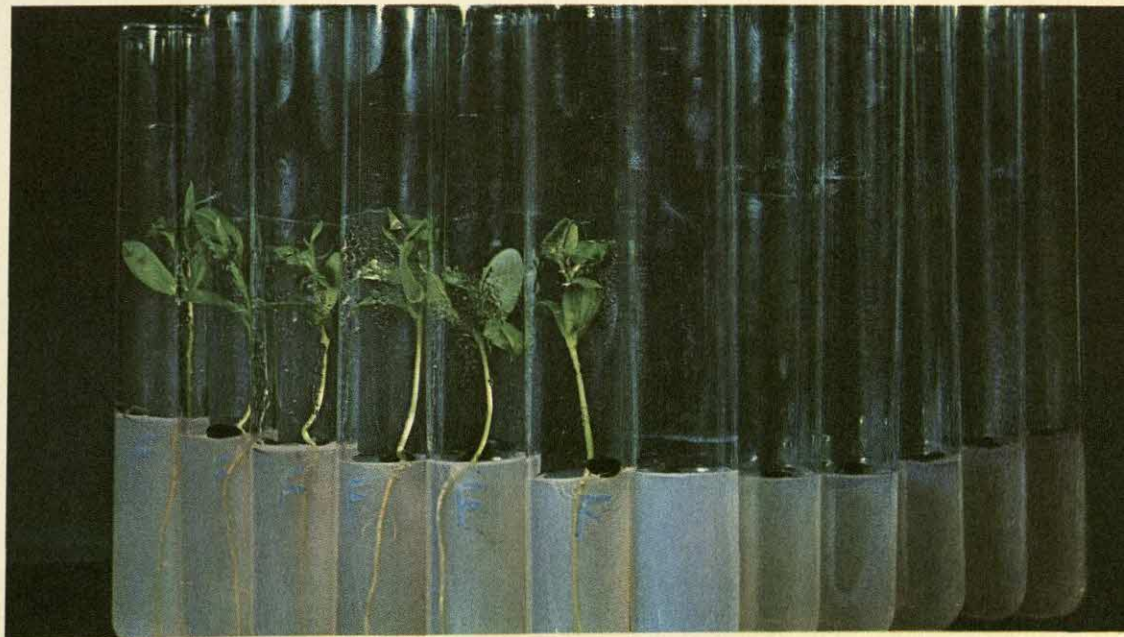
following spring, under temperature conditions which are not essentially different from those of the previous autumn. Evidently the seeds have emerged from the state of spontaneous dormancy during the course of the winter.

It has long been the practice of horticulturists to subject such dormant seed to the process known as stratification, which consists of placing the seed between layers of moist sand in the autumn and leaving it out-of-doors throughout the winter; it is then found that seed so treated will germinate readily in the spring. On the other hand, seed maintained in a greenhouse under moist, *warm* conditions throughout the winter will be found to germinate very poorly, if at all. It is evident, therefore, that *cold* conditions are necessary to break the dormancy of seeds such as those of apple and peach (fig. 2). It is important to note that the cold-treatment is effective only when the seeds have imbibed water—the dormancy of dry seeds is not removed by chilling.

The horticulturist has to take special measures to ensure that certain seeds receive chilling treatment to secure germination, but under natural conditions they will generally receive the necessary chilling within the normal cycle of climatic changes.

The biological advantage which arises from this chilling requirement of many seeds seems to lie in the fact that the dormant

Fig. 2. Experiment showing the innate nature of dormancy in apple seed. Twelve apple pips were sown in sterile conditions in test-tubes, on a nutrient jelly, and the tubes were sealed. Six tubes were placed in a temperature of 20°C ; the other six at 3°C for six weeks and then at 20°C . The pips in the tubes on the left, which were exposed to cold conditions, were the only ones to germinate. (Experiment by Nitsch. Photo Lod).



seeds are apparently more frost-resistant than the germinated seedlings; the fact that the seed will not germinate until it has been chilled ensures that germination is delayed until the spring, when the danger of frost and its associated drought conditions is diminished.

The embryos of seeds which normally require chilling can be induced to germinate without chilling simply by removing the seed-coat. The resulting seedlings are, however, frequently dwarfed and show abnormally shortened stems, but this dwarfism can be removed by chilling the seedlings themselves, after which they show normal growth.

When we consider other types of organ, such as the resting-buds of woody plants, we find a close parallel with the situation in seeds. Resting-buds are commonly formed during the late summer and early autumn—the shoots of trees cease growth and form terminal resting-buds at a time of the year when conditions of light-intensity and temperature are still quite favourable for growth. The resting-buds formed in the late summer and autumn remain dormant throughout the winter and normally resume growth in the following spring. Here, also, winter-chilling is frequently the factor which removes the dormancy of the buds and enables them to resume growth when warmer conditions prevail in the spring. If plants of various woody species are maintained in a warm greenhouse throughout the winter they fail to resume growth in the spring, whereas if they are allowed to remain out-of-doors for a few weeks during the winter, they readily expand their buds when they are transferred to warmer conditions. The amount of chilling required varies according to the species, but is usually of the order of several weeks.

Although the chilling requirement of resting-buds is essential to woody plants under natural conditions it sometimes presents difficulties in horticulture, particularly with peach trees grown in regions such as South Africa and California, where the temperature conditions in the 'winter' months are not low enough to meet the chilling requirements of peach buds. In such regions it is frequently found that the buds fail to expand normally in the spring; many of them remain dormant and the tree thus makes poor growth. Problems of bud-dormancy also arise in connection with the forcing of shoots of lilac and other woody plants for decorative purposes. Here it has been found that immersing the shoots in a water-bath at *high* temperature (35°C) for several hours is effective in breaking the dormancy of the buds. Several chemical

agents, such as thiourea and ethylene chlorhydrin, are also effective in breaking the bud-dormancy in many species.

Other resting organs which show dormancy removed by chilling include corms (eg of *Gladiolus*), the root-stocks of rhubarb and the rhizomes of lily-of-the-valley (*Convallaria*).

Although the physiological basis of dormancy has been studied for many years, we still have little understanding of its causes and of the way in which it is removed by chilling.

It is clear that growth must be inhibited in some way in dormant organs. Growth-inhibiting substances have, indeed, been shown to be present in many dormant tissues, such as potato tubers, tree buds and seed, and it has been argued that it is these substances which are responsible for the inhibition of growth in such tissues. This is only circumstantial evidence, however, and does not constitute proof that the inhibitor controls dormancy. Another possible line of approach has arisen from the discovery that gibberellic acid will break the dormancy of many buds and seeds which normally require chilling. Thus it is possible that both inhibitors and naturally-occurring gibberellins are involved in the control of dormancy, and that the effect of chilling may be to increase the gibberellins to a level which overcomes the effect of the inhibitors.

Vernalization

Dormancy phenomena are not the only processes which are controlled by chilling—winter-cold also profoundly affects the flowering behaviour of many plants in the following summer. It has long been suspected that winter-chilling promotes the flowering of many species. The experimental study of the subject began with the work of Gassner, a German botanist, in 1918. Gassner made a study of the effect of chilling on the flowering of cereals, particularly rye. It is well known that many cultivated cereals exist in 'spring' and 'winter' forms. Spring wheat and rye are normally sown in the spring and flower in the same year, whereas the winter forms are normally sown in the autumn and flower in the following summer. If winter rye is sown in the late spring it grows actively but remains in the vegetative condition and fails to produce ears. Gassner showed that the subsequent flowering of winter rye is markedly affected by the temperature conditions under which the seed is germinated (fig. 4). Plants



Fig. 3. The Canadian poplar shows vigorous growth when the days are longer than a certain minimum (above). But growth stops when the plant is submitted to a maximum of ten hours' daylight daily for a fortnight (below). The stem

stops growing; the primordia formed by the buds change into scales, not leaves, and the tree enters a state of dormancy. These illustrations show how plants react at the approach of winter when the days are shorter. (Photos Lod).





Fig. 4. Left: winter rye that has always been in a hot-house, and has produced only grass. Right: winter rye which underwent two months of cold (5°C) after germination, before being put in the hot-house, where it has produced ears. (Experiment by Nitsch. Photo Lod).

germinated at 1-2°C produced ears normally, whereas plants germinated above 5°C produced very few or no ears. On the other hand, the temperature during germination had no influence on the flowering of spring rye. Gassner concluded that whereas spring rye is independent of any need to pass through a cold period before it can produce ears, the flowering of winter rye depends on its receiving a chilling treatment. He further showed that the cold period could be given either during germination or to leafy seedlings at a later stage of development. In following up this work, Lyssenko showed that the chilling treatment can be given at a very early stage of germination, and he developed a technique in which the seeds were allowed to take up a minimum quantity of water to permit swelling of the grain and slight growth, but not sufficient to permit further germination. (The chilling treatment is not effective with completely dry seed.) The seed could then be chilled effectively so that it flowered when subsequently planted and grown. It was possible by this technique to give the necessary chilling treatment at such an early stage of germination that the normal mechanical methods of sowing the grain after treatment could be followed; this technique was called 'jarovization' or 'vernalization'. In this way the sowing of winter cereals could be delayed until the spring and flowering still obtained in the same year. It was at first claimed that the use of vernalized winter wheat in this way had advantages over spring wheat, but subsequent experience seems to have indicated that the economic advantages of vernalization are slight.

It should be noted that flower primordia are not formed during the actual period of chilling but appear only some time later. This means that there is a 'carry-over' effect of the chilling treatment in vernalization. The change from the vegetative to the flowering condition occurs at the growing points, which are switched from producing leaves to producing flowers. In vernalization, therefore, the effect of chilling on flower formation shows 'delayed action'. The possible basis of this mechanism is discussed below.

It is now known that the flowering of many other species besides winter cereals is controlled by winter-chilling; among these are many biennials, such as foxglove (*Digitalis*), henbane (*Hyoscyamus*), sugar beet (*Beta*), celery (*Apium*), carrot (*Daucus*) and cabbages (*Brassica*). These are plants which normally remain vegetative throughout the first season of growth if they are sown in the spring, and

flower in the second spring or summer. If they are protected from winter-chilling they fail to initiate flowers and may remain permanently vegetative (fig. 5), as is known to be the case with cabbages grown in localities which have very mild winters. Some of these biennial species can be vernalized either in the seed stage (as in cereals) or at a later stage of growth (eg sugar-beet), while others can be vernalized only when the seedlings have reached a certain minimum size (eg cabbage, carrots).

In addition to biennials, many perennial plants behave similarly, for instance perennial rye-grass (*Lolium perenne*), cocks-foot (*Dactylis*) and many other grasses, carnation (*Dianthus*), wallflower (*Cheiranthus*), certain primulas and scabious (*Scabiosa*). Another good example is the garden chrysanthemum, certain varieties of which have a vernalization requirement and will not flower unless the young shoots are chilled. The new shoots which arise at the base of the flowering plant in the autumn, and which will form next season's flowering shoots, are themselves unvernallized and the 'stools' thus require vernalization afresh each year.

The chrysanthemum also furnishes a good example of the interaction between vernalization and photoperiodic effects; it is a short-day plant, and forms flowers in response to the decreasing day-lengths of August. Those varieties which also have a vernalization requirement therefore need both chilling and short days for flowering. Similar interactions between day-lengths and temperature effects are found in certain long-day plants; thus henbane and rye-grass require both vernalization and long-day conditions for flowering. Such plants receive their vernalization treatment in the winter, but flower-initiation cannot occur until day-length reaches a certain minimum in the spring.

It has recently been discovered that winter-chilling controls reproduction not only in flowering-plants but also in many bryophytes, including both mosses and liverworts. In these plants, also, both temperature and day-length are frequently involved.

A great deal of effort has been directed towards elucidating the physiological processes underlying vernalization, but it must be admitted that we are still far from an understanding of the subject. A number of important results have been obtained, however, and these are enabling us to define more clearly the nature of the problems which are involved.

These findings may be summarized briefly as follows:

- (1) It seems clear that vernalization involves metabolic processes, as shown by the fact that the seed must have imbibed water, and that oxygen and a supply of sugar are necessary, presumably to permit the operation of respiratory processes.
- (2) The processes occurring during the vernalization of rye are known to take place in the embryo itself and not in other parts of the grain.
- (3) Although the vernalized condition can be destroyed by subjecting the seeds to high temperature treatment immediately following chilling, if such treatment is delayed the vernalized condition seems to have become 'fixed' and is then difficult or impossible to reverse.
- (4) With few exceptions, the vernalized condition cannot be transmitted by grafting, as can the 'flower-hormone' in photoperiodicity.
- (5) There is a marked 'after-effect' of chilling treatment, as already explained.

These observations have led to the hypothesis that the processes involved in vernalization take place in the meristematic cells of the growing point itself, and that once established the vernalized condition can be transmitted through many cell-generations by cell-division. Thus the vernalized condition is apparently self-perpetuating. Since there is no evidence that vernalization brings about any nuclear genetic changes, it must be concluded that the changes involved are located in the cytoplasm and that vernalized cytoplasm is transmitted to the daughter cells in cell-division. All attempts to identify the nature of the cytoplasmic changes have so far proved unsuccessful, and attempts to extract specific flower-inducing substances from vernalized tissue have met with success in one or two cases only (see fig. 1, page 82).

Another line of attack on this problem has recently been opened up, however, with the discovery of gibberellins as natural plant hormones. It has been found that certain plants, eg biennial henbane, which normally

require chilling for flowering, can be induced to flower *without* vernalization if they are treated with gibberellic acid. Thus gibberellic acid can be substituted for chilling treatment. Since the gibberellins are known to be widely distributed among higher plants, this observation suggests that possibly the effect of vernalization is to increase the natural gibberellin content of the chilled plants, and this hypothesis is being actively investigated. However, gibberellic acid cannot replace chilling treatment in all species which require vernalization, and it seems certain that gibberellins cannot provide the complete answer to this problem. Many plants which have a vernalization requirement remain in the rosette stage unless chilled, but after vernalization they 'shoot', ie the stem undergoes active extension at about the same time that flowers are formed. In some species the unvernallized plants respond to the application of gibberellic acid by 'shooting' in this manner, but they do not form flowers. This seems to indicate that flower-initiation and shooting are two distinct effects of chilling, and that the effect of gibberellic acid is primarily to induce internode extension. Where flowering also occurs it seems to be a secondary effect.

We have thus seen that winter cold has several diverse effects on plants—the breaking of dormancy in seeds, buds, tubers, etc, the induction of flowering in many species, and the stimulation of stem extension. There is some evidence that these diverse effects are controlled by similar physiological processes, as shown, for example, by the effects of gibberellic acid on both dormancy and flowering. Nevertheless it seems highly probable that the promotion of flowering by chilling is the result of certain specific processes not involved in dormancy phenomena.

Although we still await answers to many physiological problems such as how winter cold exerts its various effects, there is no doubt that the annual cycle of temperature changes has had a most profound influence on the form of plants during their evolution, and that it still continues to influence their development at all stages of the life-cycle.



Fig. 5. Carrots need winter cold in order to flower. Right: a carrot that has had winter chilling and so has flowered. Left: a carrot that remains in the vegetative state because it has not had winter chilling. (Experiment by Nitsch. Photo Lod).

Photoperiodicity

R. J. DOWNS and W. L. BUTLER

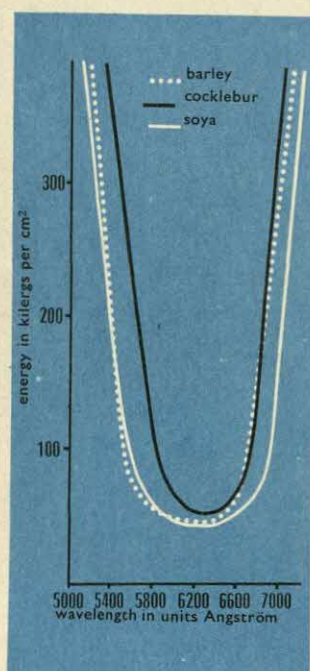


Fig. 1. Graph showing the effect of light of different wavelengths on barley, cocklebur and soya bean.

Plants detect the onset of the different seasons of the year and respond to it in ways that we have come to accept as normal, often without inquiring why the response occurs. As the winter season draws to a close and the warmer weather of spring arrives, seeds germinate and produce new plants, new leaves appear from the tubers and bulbs of herbaceous perennials, and the dormant winter buds of trees and shrubs swell, open, and form new leaves. Some plants flower in the spring, others in midsummer, and still others in the autumn. In late summer or autumn, usually well before the cold temperatures of winter arrive, trees and shrubs stop growing, form buds, and prepare for winter.

How do plants detect the seasons and what mechanism do they use to respond to it? In 1920, W. W. Garner and H. A. Allard answered the first part of this question when they reported that the relative lengths of the day and night controlled the flowering and dormancy of many kinds of plants. They called this phenomenon 'photoperiodicity'.

As soon as the discovery of the photoperiodic control of flowering and dormancy was reported, commercial growers, plant breeders, pathologists, and many others began to use the response to day-length as a tool for profit and research without knowing the answer to the second part of the question. For example, the chrysanthemum, growing under natural conditions, is an autumn crop.

The chrysanthemum begins to grow in the spring and continues vegetative growth throughout the long days of summer. In late summer or autumn, as the days become shorter, flowers are initiated and developed on plants large enough to produce commercially acceptable flowers. This same sequence of day-lengths is now obtained artificially at any time of the year by lengthening or shortening the natural light period. Chrysanthemum flowers now are produced every week of the year. Poinsettias, which, like chrysanthemums, flower when the days are short and the nights are long, are produced in a prime condition of flowering precisely at Christmas, by artificially lengthening or shortening the naturally-occurring light periods.

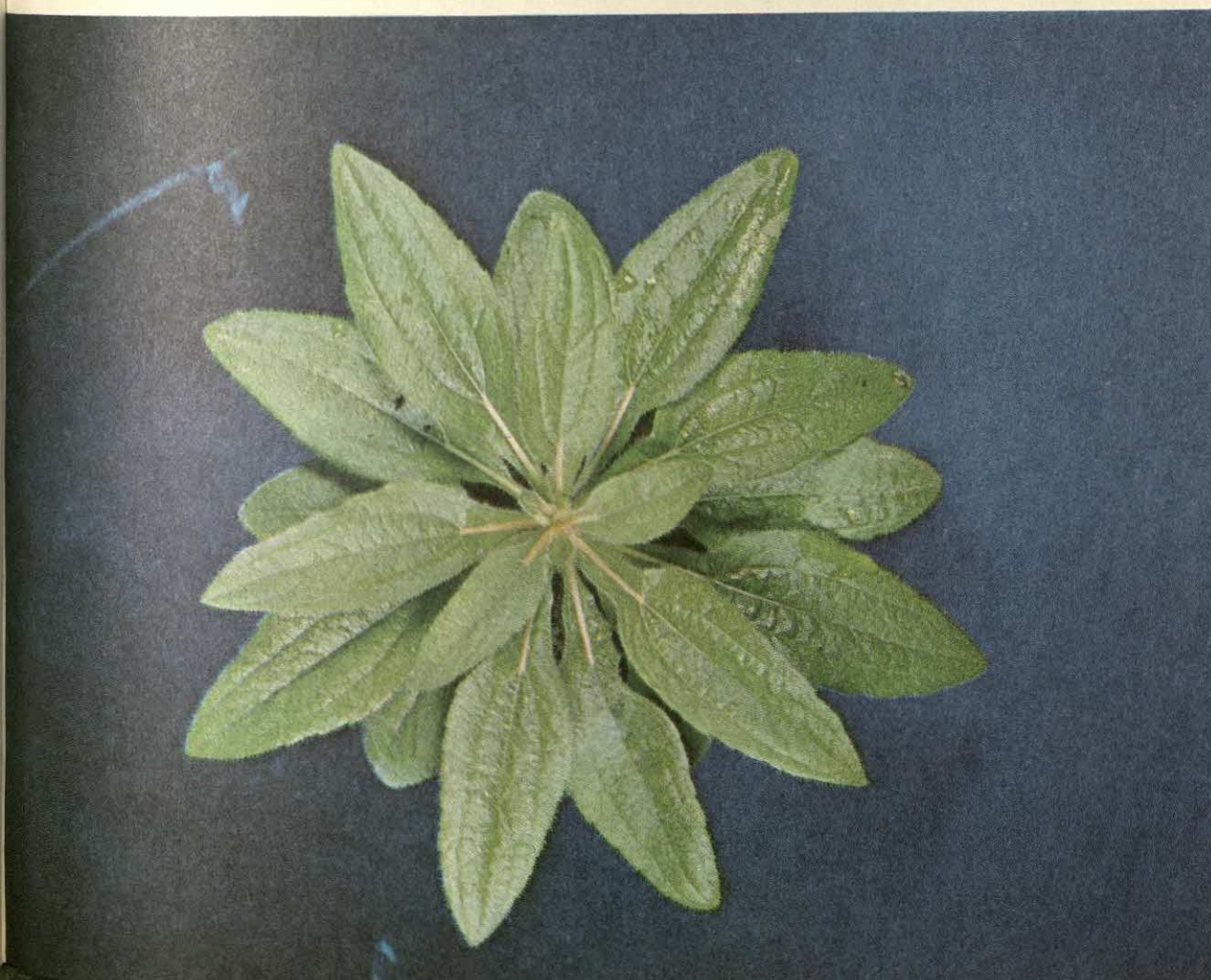
Plant breeding can be accomplished only if the selected parental stocks flower at the same time. By controlling the lengths of the daily light and dark periods, plants that normally flower at widely different times of the year can be brought into flower simultaneously.

Pathologists have used artificially long days to keep woody plants growing actively throughout the winter in the greenhouse, and entomologists have used the same technique to ensure a supply of tree leaves during the winter months for feeding experimental insects.

Plants apparently measure time because they react differently to the long days of summer and the shorter days of autumn. Plants actually measure the duration of



Fig. 2. The apical meristem of *Rudbeckia speciosa* produces a flower (above) when nights are short (8 hours), but leaves (below) when nights are long (14 hours). (Experiment by Harada. Photo Lod).



Two *Rudbeckia speciosa* plants of the same age. Left: elongation of the stem under short-night conditions. Right: extreme shortening of the internodes under long-night conditions.

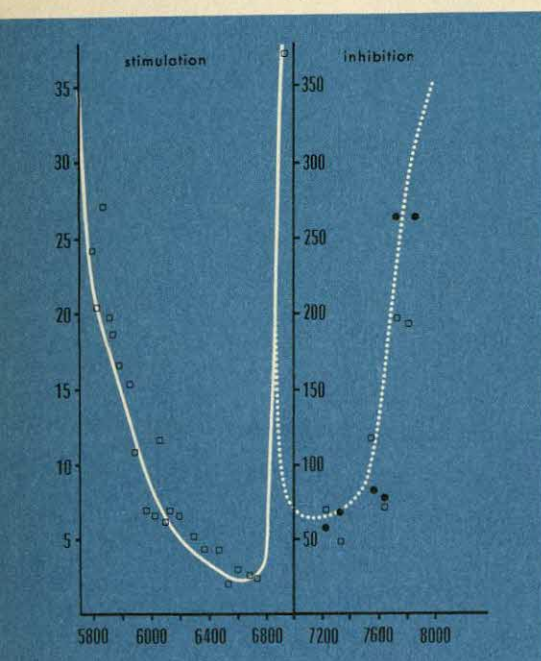


Fig. 3. Graphs showing stimulation and inhibition of germination of seeds of 'Grand Rapids' lettuce. Left: stimulation after a 16-hour period of imbibition in the dark. Right: inhibition after a 16-hour period of imbibition in the dark followed by 98 per cent stimulation by red radiation. Horizontal axis: wavelengths in Angstrom units. Vertical axis: energy required for 50 per cent germination. (In watts $\times 10^{-3}/\text{cm}^2$).

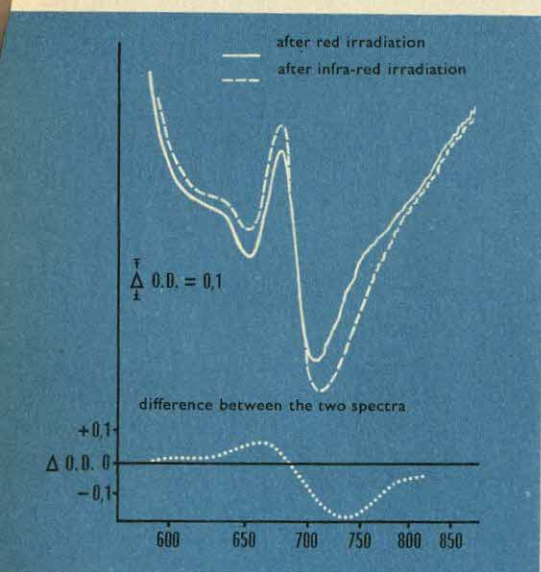


Fig. 4. Graph showing the difference between the absorption spectra of etiolated (dark brown) maize seedlings after exposure to red and infra-red light.

darkness, and the main function of the light period is to operate the photosynthetic machinery. If a long dark period is interrupted with a brief interval of light, summer-flowering plants, such as barley, flower as though they were receiving long days and short nights. The same treatment given to autumn-flowering chrysanthemum plants inhibits flowering. If the light period is interrupted with an interval of darkness, no measurable change occurs in the flowering response.

The mechanism of photoperiodicity

In order for light to be photochemically effective in producing a physiological response, it must first be absorbed by a special kind of chemical compound within the plant. Those colours (wavelengths) that are absorbed most readily by this compound are usually the most effective in producing the response. We can determine the 'effectiveness' spectrum, generally called the action spectrum, by measuring the energy of light at different wavelengths required to produce the plant response. The action spectrum is related to the absorption spectrum of the compound involved.

The action spectrum for the photoperiodic control of flowering was determined by giving short-day plants a brief illumination of monochromatic light near the middle of their long, flower-inducing nights. This was accomplished by placing the plants, defoliated to a single leaf, across the spectrum obtained from a large spectrograph. White light passing through the prisms of the spectrograph is broken into its component colours to give a continuous spectrum of known energy. The action spectrum for 50 per cent inhibition of flowering of short-day Biloxi soya beans (fig. 1) shows that red light in the region of 660 $\text{m}\mu$ is the most effective. Action spectra for cocklebur and other short-day plants show the same maximum effectiveness of red light.

Flowering of short-day plants is inhibited by a dark period interruption, whereas flowering of long-day plants is promoted under these conditions. Action spectra for the promotion of flowering of barley and other long-day plants are the same as the action spectra for the inhibition of flowering of short-day ones. The similarity of action spectra shows that flowering of both long- and

short-day plants is controlled by the same compound.

The photocontrol of elongation of stems was recognized three centuries ago, but little was known about the mechanism of this control. Action-spectrum studies established that the elongation of stems was controlled by the same light-reaction that regulates the flowering of photoperiodically sensitive plants. The germination of light-sensitive seeds and the coloration of various plant tissues are also controlled by this same system. Studies by L. H. Flint and E. D. McAlister in 1935 showed that red light promoted germination of light-sensitive lettuce seeds but that far red or near infra-red inhibited germination. Detailed investigations by H. A. Borthwick, S. B. Henricks, E. H. Toole and V. K. Toole showed that the action spectrum for seed germination was essentially the same as that for flowering and that for stem elongation. This is shown in fig. 3 (left), where the energy required to produce 50 per cent germination is plotted against wavelength.

Further studies demonstrated that the promotive action of the red light was reversed by a subsequent exposure to far red. Lettuce seeds, which had been promoted to maximum germination by an exposure to red light, were irradiated with monochromatic radiation from the far-red region of the spectrum. The action spectrum showing the radiant energy required to reinhibit germination to 50 per cent is shown in fig. 3 (right). Wavelengths in the region of 735 $\text{m}\mu$ are the most effective in reversing the action of red light. The system is repeatedly reversible, so that after a series of alternate exposures to red and far red the response is determined by the kind of light given last in the series. If red is given last, the seeds germinate, but if far red is given last, germination is inhibited.

Flowering, elongation, and fruit coloration were re-examined to determine whether the reversal of the red light action by far red was a general characteristic of the control mechanism. In each case the reversibility was demonstrated. Thus, photoperiodicity is only one manifestation of a photoreaction that controls a large number of plant responses. This photoreaction is of universal occurrence in plants, although its control may be displayed by one response in one kind of plant and by a different response in others. For example, the photoreaction controls the flowering of the cocklebur plant but not the germination of its seeds, and although the photoreaction does not regulate flowering in the

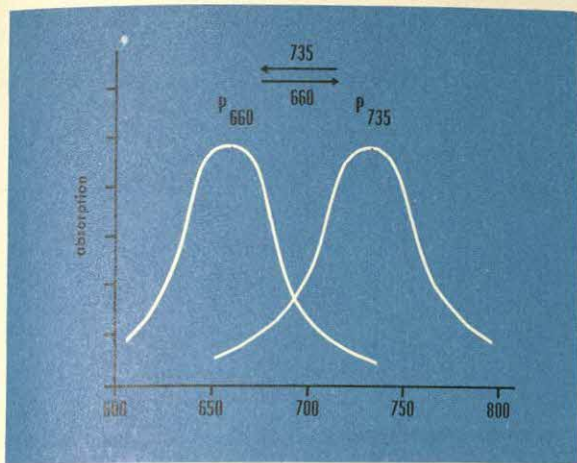


Fig. 5. Absorption spectra of the two forms of phytochrome: P_{660} and P_{735} (in millimicrons).

tomato in certain varieties, it controls the coloration of the fruit and the germination of the seeds.

The physiological investigations showed that the light-absorbing compound in the plant exists in two forms: a red-absorbing form P_{660} , and a far-red-absorbing form, P_{735} (fig. 6). When P_{660} is irradiated with red light, it changes into P_{735} . P_{735} , when irradiated with far-red light, reverts to P_{660} . The evidence indicates that the far-red-absorbing form is active enzymatically in a biochemical process so basic to plant metabolism that it can control a wide variety of plant responses. The red-absorbing form is the means by which the plant can keep the potentially active enzyme in a quiescent state awaiting activation by red light. This red-, far-red-reversible substance has been called 'phytochrome'.

The absorption characteristics of the two forms of phytochrome and its unique reversibility were known in 1952. However, the problem of detecting the phytochrome by physical or chemical means within the tissue or of extracting it from the tissue proved to be a difficult one. The most sensitive test appeared to be a spectrophotometric one based on the changes in absorption spectra which accompany the reversible changes of phytochrome form. But phytochrome is present in very low concentration and its spectroscopic detection had to await the development of spectrophotometers which could measure, at high sensitivity, the light transmitted through dense, light-scattering samples such as plant tissue. The direct measurement of the absorption of light by phytochrome was first demonstrated in 1959 with spectrophotometers developed by K. H. Norris. Fig. 4 is a difference spectrum obtained

with a sample of three-day-old, dark-grown maize seedlings. The absorption spectrum of the sample was recorded after an exposure to red light, which put the phytochrome in the far-red-absorbing form. The sample was then irradiated with far red to change it into the red-absorbing form and the spectrum was recorded again. The difference spectrum, which is the difference between the absorption spectra of the far-red-irradiated and red-irradiated samples, showed that the far-red irradiation caused a decrease in an absorption band with a maximum near 735 $m\mu$, while an absorption band at 660 $m\mu$ increased. This change was repeatedly reversible by alternate exposures to red and far red. Thus, the two photoreversible forms of phytochrome were clearly demonstrated and their absorption maxima precisely matched their action maxima. Phytochrome has been detected in a wide variety of plant species and appears to be of universal occurrence. The highest concentration of phytochrome seems to occur in seedlings grown in complete darkness.

The reversible absorption changes constituted a practical test which permitted phytochrome to be separated from the plant

Fig. 6. Diagram showing the germination of four lettuce seeds of the 'Grand Rapids' variety. Left: no germination in dark conditions. Left centre: no germination with infra-red light of 7,350 $\text{\AA}$ wavelength. Right centre: germination takes place with less than one joule/cm² of red light at 6,600 $\text{\AA}$ wavelength. Right: illumination with infra-red light, given immediately after exposure to red light, totally reverses the effect of the red light and inhibits germination. (Preparation by Nitsch. Photo Lod).



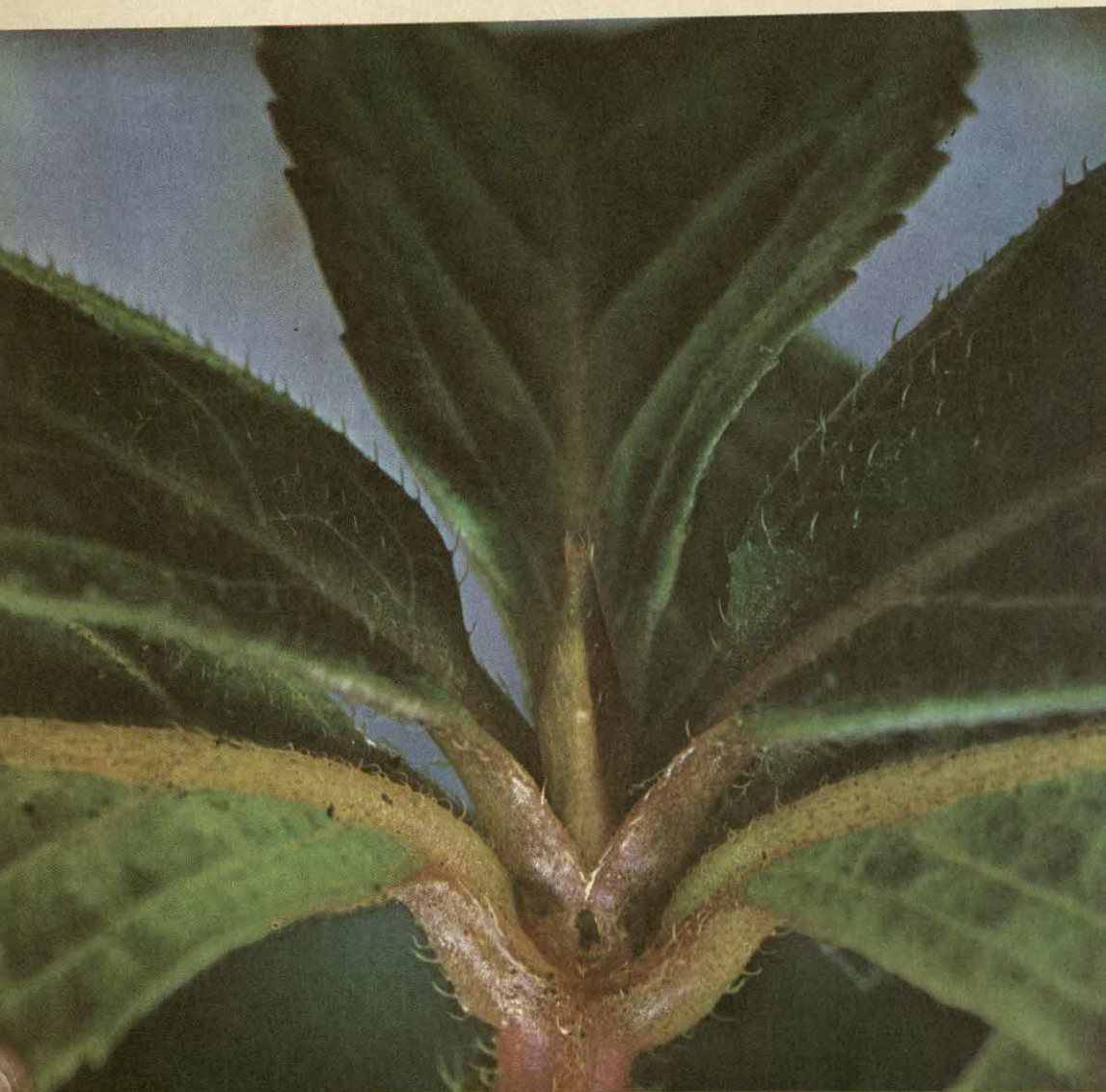


Fig. 7. The shrub *Weigela florida*. Growth stops completely when long nights (14 hours) alternate with short days (10 hours) because of inhibition of internodal extension and of the growth of leaf primordia. The latter produce scales instead of leaves (above). The apical bud grows vigorously if the plant is exposed for half an hour of fluorescent light in the middle of a long night (below). (Photo Lod).

material. A double-beam difference spectrophotometer, which directly measured the difference in optical density between 660 and 735 m μ , was more convenient than the scanning spectrophotometer for this test. Phytochrome was extracted from dark-grown maize seedlings with an alkaline buffer at pH 8 and the phytochrome remained reversible. Further studies showed that phytochrome is a soluble protein that can be partially purified by precipitation with ammonium sulphate at 33 per cent saturation. Denaturation of the protein leads to a loss of reversibility. Purification of phytochrome is currently in progress.

The spectrophotometric test permits measurement of phytochrome changes within the intact plant (*in vivo*). Physiological experiments had indicated that the far-red-absorbing form of phytochrome was slowly converted back into the red-absorbing form in darkness, whereas the red-absorbing form was stable. This has been confirmed by direct measurement. In dark-grown material phytochrome was found entirely in the red-absorbing form. Dark-grown maize seedlings were given a brief irradiation with red light to convert the P₆₆₀ to P₇₃₅ and examined at various times thereafter to determine the form of the phytochrome. During the course of about four hours at room temperature the P₇₃₅ was converted back to P₆₆₀ in the dark. The dark conversion is an enzymatic process, which is markedly slowed by lowering the temperature and does not occur at all in the absence of oxygen. In the partially purified extracts both forms of phytochrome are stable. The dark conversion of phytochrome *in vivo* provides the plant with a means of sensing time and is probably the basis by which the plant distinguishes long nights from short nights.

Studies of the photoperiodic mechanism have only just begun, but each additional increment of knowledge brings us closer to an understanding of this mechanism that controls so many diverse plant responses. An understanding of this control device will add immeasurably to our understanding of how light influences seed germination, plant growth and flowering, of the processes leading into and out of dormancy and, in fact, of plant metabolism in general.

Plant communities

Georges LEMÉE



No field botanist or lover of wild plants can have failed to observe that a particular species lives in association with a few other species, always more or less the same, gathered together in a fairly uniform floristic community. Thus the vegetation of a region appears as a mosaic of communities floristically and physiognomically distinct.

The problems of plant associations (phytosociology or phytocoenology), are complex and various. First, the communities have to be observed, defined and classified, which constitutes descriptive phytosociology; then must be determined inter-relations and the factors responsible for their localization and evolution, which is more specifically the field of synecology.^{1, 2}

Two quite different criteria can be used to describe groups of plants, one physiognomic, the other floristic.

Phytogeographers have been trying to rationalize the methods describing the physiognomy of vegetation since the beginning of the nineteenth century. The scientific basis rests on Darwin's ideas of selection by environment. Generally speaking, the form of a species is modified very little by environment, since this is the function of heredity. However, the distribution of species is greatly affected by environment, which may serve to eliminate or promote species, according to their various morphological properties.

Trees, for example, do not become established on high mountains in the temperate zone because of the short period of active vegetative growth and the action of wind and snow. Naturally, not all the morphological properties have the same importance in the adaptation to surroundings. The most impor-

tant are those that define 'life form', a term used to describe the morphological adaptation of a plant to its environment. This is not necessarily connected with its taxonomic affinities;³ species whose classifications are very different may be remarkably similar in form, such as *Cereus* and the cactus-like *euphorbias*; on the other hand, different species of the same genus may belong to very different life forms, such as the *euphorbias*.

A plant community is almost always composed of several associated life forms; one or two of these predominate by their volume and density, and so impose on the group their typical seasonal physiognomy.

A group of communities with the same predominating life forms, constitutes a *formation*, or, as this term has been given different meanings, *type of vegetation*. A forest, without further definition, does not constitute a formation but a whole family of formations, because different trees belong to different life forms. On the other hand the deciduous forest of the central European plains, which has a quiet winter period, is quite distinct as a formation from the forest of evergreen Mediterranean trees with their coriaceous leaves, or from the conifer forest of the far north, such as the taiga of the USSR.

Several centres of phytosociology have devised methods based on floral criteria which

(1) The term 'ecology' was coined in 1869 by the German biologist Ernst Haeckel (from the Greek 'oikos', meaning house or dwelling) and he defined it as 'the science of the relations between the organism and the outside world, that is, broadly, the science of the conditions of existence'.

(2) 'Synecology studies the relation of communities of organisms with their environment, in which various climatic, edaphic and biotic factors play a part; in other words, it seeks to define the habitats of the communities and their ecological range, that is to say, the variation and limits of the factors affecting the habitat' (E. du Rietz).

(3) Taxonomic affinity: the morphological relationship, which is used as a basis for the classification of plants (taxonomy).

(4) The notion of association as it is understood in western and central Europe was defined for the first time by Flahault and Schroeter at the 1910 Botanical Congress in Brussels: 'An association is a group of plants of definite floristic composition, with a uniform physiognomy and growing in uniform conditions of habitat. The association is the basic unit of synecology.' In 1915 Braun-Blanquet emphasized the importance of the floristic criteria when he spoke of an association as 'a stable group of plants in equilibrium with its surroundings, characterized by a definite floristic composition, with certain exclusive or almost exclusive elements (characteristic species) which define a particular autonomous ecology'.

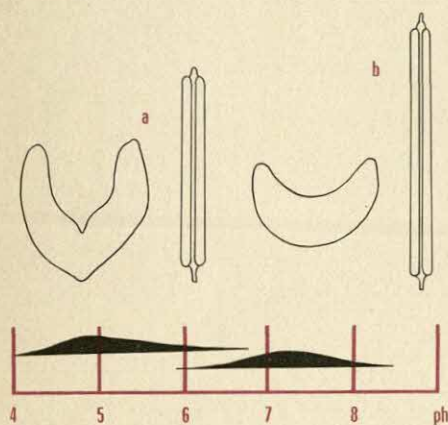


Fig. 1. Two varieties of *Carex curvula* All. showing some distinct morphological characteristics (leaf section and size of stamens) and distribution according to the soil pH.

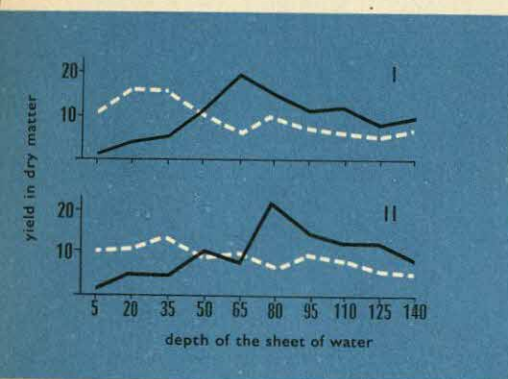


Fig. 2. Graphs showing the yield in dry matter of grass cultivated in soil with a water table graduated in depth, either in pure populations (---), or in a population composed of equal numbers of plants combining 6 species (—). I. *Arrhenatherum elatius* shows a displacement of its optimum yield towards a less humid soil, under conditions of competition between species; II. *Bromus erectus* shows a very pronounced optimum in comparatively dry soil.

have often been taken up in their respective countries. The basic units embracing areas covered by populations composed of the same flora (according to the criteria in use) have received various names, association,⁴ eg society, community, phytocoenosis; but several of the terms have other connotations.

Inventories of species are generally limited to the most abundant higher plants or their aggregate, which form but a tiny proportion of the host of organisms living together. The reasons for the composition, location and evolution of these communities of organisms, may be fully worked out only if analysis is made of the physical and chemical conditions of the abiotic environment⁵ in which they live and with which they constantly exchange matter and energy. The concepts of biocoenosis and the ecosystem⁶ have clarified this relationship.

British and American ecologists have developed the notion of the ecological system or ecosystem (a term created by the British scientist, Tansley, in 1935) which deals with the functioning of the community in relation to its food and energy. An ecosystem consists of: (1) *producers*, autotrophic organisms (essentially green plants), which enrich the system with organic substances made out of simple mineral materials; (2) *consumers*, heterotrophic organisms, such as animals, which appropriate to themselves the organic molecules of either the producers or other consumers; (3) the *decomposers*, such as bacteria and fungi, which break down the organic compounds and produce simple substances which may be used by the producers; (4) the organic and mineral substances of the environment which are at the disposal of the organisms. A lake, a pond are comparatively simple and well-defined ecosystems which have therefore been studied extensively.

Relations between plants and their environment

Ecology, usually divided into autecology⁷ and synecology, is the study of the relationship between living organisms and their environment or natural habitat. The autecological behaviour of plants is usually studied by cultivating them singly in pots. In this way physiological experiments can be carried out under controlled conditions, and strictly ecological observations can also be made under natural conditions. In the first case both the limits and the optimum conditions can be

established for the various environmental factors at work in the growth, successive phases of development, and physiological processes such as transpiration and photosynthesis; the second method gives information on the overall reaction of the plant to the complexities of the conditions offered by the physical environment.

The study of autecology leads to the conclusion that although a given plant community may have a uniform environment, it is composed of species of differing autecological behaviour, provided that the physical and chemical characteristics of the environment are within their limits of tolerance. Thus the weeds found on well-drained siliceous sand belong to species that are calcifuge as well as indifferent to lime, acid-loving and tolerant to pH, sand-loving and indifferent to the texture of the soil, with habitats dry or unaffected by damp conditions. In short, species are linked together in a community by the interplay of different causes.

Autecological studies have led to another extremely important conclusion, which is that the Linnean species includes a certain number of races which are different ecologically, although they may not be distinct morphologically; these races have been called ecotypes⁸ by the Swedish scientist, G. Turesson. Their geographical or local segregation is caused by their different reactions to surroundings. Thus there are two different sorts of Norwegian pine found in a broad belt covering the temperate and boreal regions: in the north it consists of races which need long days for growth, and in the south, races comparatively insensitive to the length of day.

In many cases, the selection of ecotypes depends on edaphic factors. For example, the races of *Carex curvula*, widespread on alpine meadows which are under snow for long periods, have recently been found to contain an acid-loving race, particularly abundant on siliceous ranges, and an alkali-loving race, which is confined to limestone ranges; as they are morphologically distinct, the first subspecies has been named *eu-curvulae*, and the second, *rosae* (fig. 1). A grass, *Molinia coerulea*, which grows in central Europe in habitats of differing humidity and acidity, sometimes in the open and sometimes in the shade, has many ecotypes in these different areas.

In natural conditions higher plants almost always live in dense colonies covering the whole surface of the ground; autecological conditions for isolated growth are found only for a short period during the initial stages on

a bare substratum, and in habitats where existence is only just possible, such as deserts, masses of debris, or shifting sands. The ecological behaviour of a plant may be favourably modified—or otherwise—by the proximity of other plants. Mountain trees like the beech, grow and reproduce better in the central part of their range when mixed with other varieties, whereas they survive only in dense clumps in the south, where the summers are hot and dry. It is well known that when several varieties of cereal are cultivated together, their relative yield differs from that obtained if each variety is cultivated separately. The experimental results of Harlan and Martini are particularly illuminating. A mixture containing equal proportions of each of eleven varieties of barley was sown on a number of plots scattered throughout the United States. A sample of the mixture of the seed harvested was sown the following year and after this process had been repeated for several years, the proportion of seed from each variety was found to vary considerably from one locality to another. In some instances a certain variety had practically disappeared, or had come to dominate the rest.

These experiments indicate that growing in the company of other forms may mean that the optimum values of the ecological factors change according to the physical and chemical properties of the environment. O. de Vries seems to have been the first to show this experimentally. He sowed several varieties of weed in parallel rows in a bed which had progressively more acid from one end to the other, and he found that they all grew equally well, although under natural conditions they have different tolerances and optima with regard to soil conditions. As the trials continued the species began to compete with one another, and the acidiphils such as *Spergula arvensis* stopped the neutrophils like *Stellaria media* from developing in the most acid areas, whereas the reverse took place in the less acid areas. In following years the underdeveloped plants were not able to form fruit and were practically eliminated from just that part of the bed where the soil acidity was far from their optimum in the natural habitat. More recent work has shown that the optimum *vis-à-vis* factors of soil acidity and humidity also changes when a plant is grown alone or mixed with other species (fig. 2).

The reasons for these discrepancies

Fig. 3. Plant associations in a beech wood. There are very few plants in the shade, but a noticeable population of ferns in the clearings. (Photo Lod).



(5) Physical (or abiotic) environment: the environment considered independently from the beings that live in it.

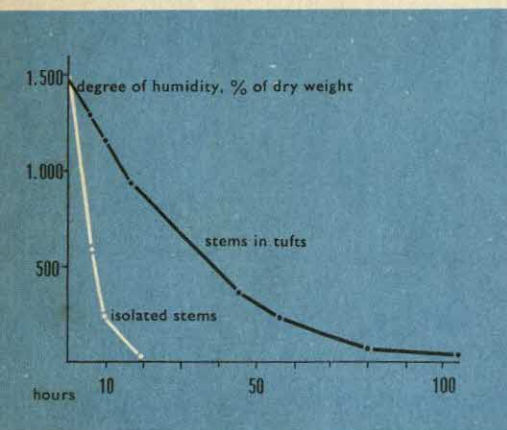


Fig. 4. Graph showing the rate of desiccation of the stems of a moss, *Hylocomium purum*, singly and in tufts. The second graph shows effective protection against desiccation (*L. Plantefol*).

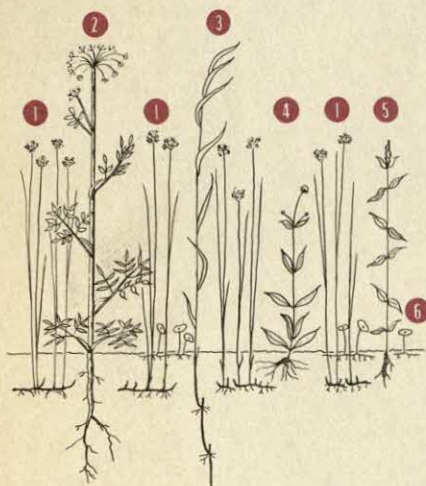


Fig. 5. Stratification of the foliage and roots of the species in a damp meadow populated with rushes. The thick network of the rhizomes of the rush, which are at the same depth, allows species with roots at greater or lesser depth to grow there as well. (1) *Juncus silvaticus*; (2) *Angelica silvestris*; (3) *Phragmites communis*; (4) *Succica pratensis*; (5) *Lythrum salicaria*; (6) *Hydrocotyle vulgaris*.

between autecological and synecological behaviour are to be found in two distinct factors. One is the modification of the physical environment by the plant population, and the other the direct interaction between the various organisms.

Effect of vegetation on the environment

Although the selection of plants is, in the first instance, influenced by the physical and chemical characteristics of the habitat, these are also modified by the vegetation, which imposes its own character on the habitat. For example, different groups of plants create their own microclimate even when local climate conditions are strictly identical. The soil profile of identical underlying rock differs, especially in its organic part, according to what is growing on it. A species growing very thickly is more efficient than single isolated plants. This mass effect is strikingly illustrated by the example of trees. Under isolated trees, at the road side or in orchards, the conditions of temperature, humidity, carbon dioxide content and even illumination are little altered, but in the confined atmosphere of the forest a distinct microclimate is created, typical of the species represented. The character of the soil under isolated trees is not very different from that of the surroundings, but in a forest the soil is covered each year by all the foliage produced, which decays *in situ* and creates an upper surface with a high humus content.

Changes in the local factors can even upset the balance with the existing community, and this creates a new biological balance, a new biocoenosis. Many examples could be quoted of the influence of a species on the evolution of the community: dunes stabilized by marram grass, heath wooded by birch trees, waste land invaded by broom, peat-bogs dried up by the accumulation of peat-moss.

To find the cause of the distribution of organisms in communities is a problem of extreme complexity.

When the atmosphere around plants alters because of their presence, this causes particular synecological effects. The most obvious examples of this, which is a phenomenon that can be measured quantitatively, are the reduction of transpiration and the increase in the amount of contained water due to the reduced rate of evaporation. *L. Plantefol* with mosses (fig. 4), and Filzer with *Phanerogams*, have shown that the loss of water from

isolated plants is greater than that from tufts, and they have measured this loss.

Interaction may also be chemical. For instance, some plants are capable of liberating substances in the soil which are either inhibitory or toxic for other species or for the seedlings of their own species. The small number of species in populations of absinth and the fact that there are no annual plants among the rosemary on Mediterranean heathlands seem to be due to this effect. Old populations of spruce and beech are toxic for their own seedlings, and this accounts for their poor reproduction and for the alternation of varieties often observed by forestry workers.

Another factor which determines the localization of a species in a particular habitat, and the prosperity of the community, is the competition which results from organisms drawing on the same sources of food and energy if these are in limited quantities. This is especially true for vascular plants as regards light, water and nutritive substances in the soil. It is keenest between individual plants of the same species and the same age growing in dense populations, for their foliage and roots are at the same level and their simultaneous requirements are identical. This is the case with most cultivated plants; their yield per acre does not increase in proportion to the density of the plants, but reaches a ceiling at a certain density. It also happens with woods consisting of a single species of the same age; if clearings are made, the annual increase in trunk thickness is greater because the trees have more access to light and to the reserves in the soil. One consequence of competition between individuals of the same species is that the weaker individual plants are often extensively eliminated. Morosov estimated the density of young trees on a ten-year-old plantation of natural unexploited beech to be about 425,000 per acre, but it was only 205 per acre in a 120-year-old forest, which indicates that one out of 2,000 had survived.

Competition between different species is more complex, but it is greater in proportion to the similarity between them in morphology and the capacity for extension. In this case coexistence is seldom possible and the variety which finds the particular conditions of the habitat best suited to it will oust the other. This is why the belts of tall grasses covering large areas around lakes and meres are usually of the same species: reed (*Phragmites*), bulrush (*Scirpus lacustris*), reed mace (*Typha*), etc. On the other hand, species with foliage and roots at different levels can live together

perfectly well, so long as one of them does not create environmental conditions which are unfavourable for the other, such as excessive shade, or the emission of toxic substances (fig. 5).

Conclusions

This brief survey of new methods and tendencies in the study of communities of organisms is an example of the new trend of thought in biology towards the concept of an integrated unit of organization and function at all levels in the study of the biosphere. These levels, in order of size, are the protoplasm, the cell, the tissues, the organs, the organism, the genetic population, the community, the ecosystem, and lastly the biosphere itself. Each unit at each of these levels is made up of units from the preceding level which associate to produce an organization and function characteristic of this unit, thus giving it its own individuality. Thus protoplasm, a cell, an organism are all entities.

We may therefore draw the conclusion that 'individual groupings as well as individual organisms are beings in the logical and mathematical sense: just as an individual organism is made up of a characteristic combination of genes, so an individual grouping is made up of a characteristic combination of species. It is remarkable that the laws governing the distribution of the frequencies of genes in a population are of the same type as those describing the frequencies of the species in associations' (M. Guinochet).

The similarities of function are as striking as the similarities of structure. Growth and metabolic processes can be equally studied at the level of the cell, the organ, the whole organism, or the community, using appropriate techniques and units of measurement. Although the knowledge gained for a given level is of great help in understanding phenomena at another level it cannot, however, explain them completely. We have shown that it is incorrect to consider growth in a population or a community of organisms to be the sum of the growth of these organisms taken in isolation; the growth of an individual grouping has its own peculiarities, and that of its constituent members isolated from it is only one element of it.

In the field of biological research, the understanding of communities of organisms is less advanced than other aspects of biology because it started later and was weakened by doctrinal controversy; its methods also are still uncertain. Its progress is none the less



Fig. 6. Secondary tropical associations on the banks of the falls of the Zambesi (Livingstone Falls) Nyasaland. In the foreground on the left, a leguminous tree; in the centre, a group of palm trees; in the background, a rain forest. (Photo Holmes-Lebel, Paris).

essential to genetics, physiology and modern systems of classification because of the importance of environmental factors and competition in the selection of form and function of the organism.

The study of communities of organisms in the field of economics is perhaps more important and more urgent still. The proper exploitation of farmland, the conservation of soil and the maintenance of its fertility, the improvement of yields are essentially problems concerning the equilibrium of the vegetation and its environment. Human intervention too often causes this balance to be disturbed, with sometimes catastrophic results; for instance, soils brutally destroyed by denuding cultivation, fire, or deforestation; loss of fertility due to indiscriminate exploitation; the introduction, voluntary or not, of animals or plants which upset the biocoenoses; pollution of the atmosphere and the water surrounding industrial centres. In face of the growth in world population, a far-sighted programme is essential in order to realize the earth's potential wealth, instead of 'putting the planet to pillage'. The part played by ecologists will be very important.

(6) Biocoenosis and ecosystem: the term biocoenosis was coined by Möbius in 1877, but the concept has been especially developed in eastern Europe. Sukatchev recently defined phyto-coenosis (the plant aspect of biocoenosis) as 'a group of plants living in a uniform area of the earth's surface, characterized by certain specific relationships not only between the plants, but also between the plants and their habitat, as a result of which a specific environment is created, namely the plant environment'.

(7) Autecology: ecology of the isolated individual as opposed to synecology (see note 2).

(8) An ecotype is composed of a population of individuals having identical reactions to the external factors; they are situated by these external factors in particular habitats and isolated from other populations of the same species. Ecotypes very often have morphological or genotypic characteristics, although they are not classified as taxonomic units; thus the taxonomic and genotypic forms of a species may constitute as many ecotypes or groups of ecotypes.

Vegetation maps

Henri GAUSSEN

To a botanist, the words flora and vegetation have different meanings. The flora is the list of plants found in a region or a place, whereas the vegetation is the plant landscape. The vegetation of a country is composed of forests and meadows, marshes and peat-bogs, or deserts.

(1) Ecological requirements: see the chapter on 'Plant communities'.

(2) Winter resting period: period during which the days are shorter than the nights (July-August in the southern hemisphere).

Maps can be made to show the distribution of each type of plant. These are floristic maps, which show the ecological requirements¹ of the plant and often raise geological problems to explain their present range.

When making a map of the vegetation, the position of the units of the plant landscape must be represented. It is with this problem that we are concerned. First comes the question of scale. More detail can be included on a large-scale map than on one with a scale of 1/200,000 or 1/1,000,000. In France the following terms for maps are current:

Map showing how the land is owned and distributed: cadastral maps.

Map of plant groups: scale 1/20,000.

Map of the vegetation: scale 1/200,000.

International map of the extent of vegetation cover: scale 1/1,000,000.

This is the scale of the only international topographical maps that can be used as a background on which to show the vegetation.

Outside France similar scales have been used; 1/200,000 is often employed. The international map known as the *Land Use Survey*, which is the map of the use to which land is put, on the basis of the vegetation, is on a scale of 1/1,000,000. Most categories of maps are drawn to these scales.

Different types of map

Maps may be found in atlases which show the whole of the world's vegetation, but they

can represent only the large units or 'zones of vegetation' which are directly determined by the climate. The most important divisions are: the equatorial forest, the tropical savannas and steppes, the deserts, the Mediterranean zones with a summer resting period, the steppes which have cold winters and resting periods both in winter and summer, the temperate zones with a winter resting period,² the conifer forests, tundras, and regions under ice. Within these various regions the climate of mountains is colder than that of the neighbouring plains.

The colouring used has not been formally agreed upon, but in general a dark shade is used for forests, a lighter shade for steppes, and often orange or red for deserts.

The following are descriptions of some maps generally used in France. They are representative of maps commonly used throughout the world.

General map on a scale of 1/5,000,000: no such map exists at present.

Map of the 'World Land Use Survey': this map, which was drawn by a committee of the International Geographical Union, shows the results of an inquiry into the use of land. Forests are divided into a number of types according to their density; different types of cultivation are distinguished, but without particular attention to botanical problems. The colouring is arbitrary.

International map of the vegetation cover pub-

synthesis of the climatic influences. The question has been studied in detail, but roughly speaking, blue represents humidity; black, cold; yellow, comparative drought; orange, extreme drought; red, great heat. The colours can be mixed in the same way as the climatic influences. For example, a hot damp equatorial forest will produce a mixture of blue and red, and on the map it will be represented by violet. The oak forests of temperate zones where the conditions are halfway between humidity and comparative drought will be shown by a mixture of blue and yellow; they will be green. For representing only the essential environmental factors, a sufficient range of colours is available.

In brief, the blocks on the map show the vegetation; the colours used give it its ecological and botanical value. Map insets provide further information on hypsometry, pedology, the climaxes, the administrative divisions, agricultural statistics, the use of the land, the principal climatic conditions, agricultural setbacks, etc. There are reference letters or signs on the map for such further detail on the vegetation as may be desired.

The vegetation map on a scale of 1/200,000. The French map published by the Survey Unit in Toulouse ('Centre national de la Recherche scientifique') is based on the same principles as the map of the vegetation cover, but is in greater detail. Aerial photographs are first used to make an outline map on a scale of 1/50,000, and after a study in the field the details are added. These maps are used as a basis for the master map from which the maps on a scale of 1/200,000 will be printed.

Some other principles have been used for this scale. For instance, the map of Switzerland is based on the concept of vegetation types. If the ranges of a great number of plants are outlined on the same map, groups appear which are obviously the result of environmental influences. This is another way of arriving at the method based on the differentiation of environments. The colours chosen for the map

of Switzerland do not follow a set scheme. The maps of Belgium, some maps of Italy, etc., are published on the same scale, and similar maps are being prepared in several countries.

Maps of plant groups. Many maps have been published by the Institute at Stolzenau-on-Weser in Western Germany, and by the Survey Unit for the mapping of plant groups at Montpellier (CNRS). These show the plant associations in units defined by floristic data. The associations are classified according to their floristic affinities, and a hierarchy is obtained which is based on the present types of vegetation unit. This is a static classification, whereas the classification by series is dynamic.

The choice of colours is along the lines of the general principles indicated above.

Maps of this kind accompany articles on phytosociology.

Uses of maps

These are the main types of map in use in the past few years, and they have a wide public. Atlases are used in general education and to teach geography and botany. Maps of the vegetation cover are essential for great international organizations and governmental economists. They are used to draw up overall plans, because they can demonstrate the scope of the plans, and so help in an estimate of the cost.

Maps on a scale of 1/200,000 or something similar are made from detailed maps on a scale of 1/50,000; they are invaluable in the organization of large-scale operations over an area of 8,000 square miles, for instance. The series plan helps in the understanding of the evolution of vegetation, whether the process is going to be assisted or opposed; it is absolutely necessary to be familiar with it in the spheres of afforestation and farming.

Large-scale maps are useful for land exploitation. Valuable information is provided about possibilities in farming or forestry, according to the types of plant association.

A view of the vegetation of the world

Pierre DANSEREAU

The biosphere, made up of living beings, more or less envelops our planet, and also penetrates it to a certain depth. It is on the surface of the continents, however, that living creatures occupy the most significant areas and play their most important part in the cycle of resources. It is this aspect of vegetation that may properly be considered first, as its foremost function is to act as an agent for the transformation of mineral and organic matter into living tissue.

The portion of the vegetation that is not eaten by animals is restored to the earth; the ways and processes of plant assimilation and decomposition form the subject of many ecological studies. On a single site, the various plants seem to work in association. There is a fixed division of function among them, so that the resources are more or less completely exploited. For instance, in a tropical savanna the roots of the grasses, whose activity is only seasonal, go deeper than those of the trees, which are active the whole year round. In each region, in the same landscape, there will be different sorts of association next to each other, with a contrast in how each is made up in bulk: for instance, a forest with several tiers, a field adjoining, with a single layer of herbaceous plants, and an outcrop of rock with a mere crust of lichen. The biological potential of these three types of plant formation is not the same. The amount of oxygen,

carbon dioxide, nitrogen, phosphorus, water, etc., that each uses in the course of a day, a season or a year, is quite different, as are the quality and quantity of the tissues formed or stored.

Although each site or region is colonized by different species (pines, oaks, laurels, palm-trees, etc.), it must be realized that each plant association with its seasonal changes is conditioned by the soil type, the climate and the history of the area. The structure of the association is determined by adjustments between the different species; the association itself will appear as a fairly stable feature in a given 'niche'¹ of the landscape. Consequently, the plant cover² of a region can be understood by considering the topography, which induces microclimatic variations, and the soil which varies the nutritive resources. On the scale of a few acres the interaction of these factors is fairly intelligible, the main features being the system of drainage, mineral content of different underlying rocks, random dispersion of the species, etc. But on a smaller scale, these physiological factors characterizing and defining the different associations of plants are no longer distinguishable, and only the main features of the vegetation are apparent.

On a world scale, how many types of vegetation are there, or rather, which type is characteristic of each region? We can classify vegetation according to its characteristics,

(1) Niche: *in this sense, a unit defined by the particular conditions of the environment.*

(2) Plant cover: *all the plants which cover a geographical area.*

(3) 'Climax': *the more or less stable plant population, the final result of the evolution of the vegetation from an originally empty area; it is determined by the combined effect of the soil and the climate. The corresponding adjective is climactic (and not climatic).*

(4) Edaphic: *related to the soil.*

(5) Subsidiary types of vegetation are subject to the overall influences leading to the 'climax', but are distinguished from it by a more or less limited local factor.

(6) Sclerophyllous: *with more or less leathery leaves.*

(7) Mangrove: *type of forest found on the sea coasts of tropical countries, especially those with lagoons, exposed to the action of the tides.*

(8) Epiphytes: *non-parasitic plants, which require support but not food from their hosts.*

(9) Laterization: *age-long transformation of the soil in rainy tropical regions, where intense leaching combined with the high temperature carries away the silicate ion (which forms clay) and leaves behind an excess of alumina hydrate.*

(10) Podzolization: *age-long transformation of the soil in rainy temperate regions into grey 'podzol', which is the result of leaching of the bases of the original soil, and the formation of a deep deposit or concretion containing iron oxide especially.*

Fig. 1. The Sahara, a hot dry desert. The photograph shows Beni-Abbes in the valley of the Saoura, where water flows only once a year, when rain falls on the distant Atlas mountains. A palm-grove draws life from the scanty springs at the foot of the dunes of the Erg. In the distance is the desert plateau or Hamada, where annuals grow once every 3 to 5 years, when there is an exceptional fall of rain. (Photo P. Chouard).



but it is helpful to also know the forces governing the distribution of the formations, and the climatic conditions. Though the exact part played by temperature and rainfall in the grouping of species and associations is still very uncertain, the main types of climate in different parts of the globe produce almost identical features. For instance, a treeless vegetation called tundra is found both in the very cold Arctic zones and on high mountains; extremely hot and dry countries throughout the world are characterized by woody plants, succulents, and annuals that are very scattered (desert), etc.

Vegetation has thus been classified on the basis of the following criteria: (1) the woody and herbaceous components, (2) the height, mode or density of the covering, (3) the periodicity and type of leaf. Each category is used as a sort of index of a type of climate which is fairly widespread geographically and is found the most often in several parts of the world.

A complete picture of each of these types would include the following: a description of the structure of the 'climax'³ or 'climactic vegetation', i.e. the vegetation on well-drained sites, apparently permanent; a reference to

the climatic and edaphic⁴ conditions, i.e. the principal influence of the climate and the soil; a list of the subsidiary types of vegetation⁵ found on the driest and wettest sites, or as a result of human intervention; and a reference to the utilization of the land and its cultivation by man.

The so-called subsidiary vegetation may be very similar from one region to another; for example, a dune or a marsh in sclerophyllous⁶ forest conditions and in coniferous forest conditions differ far less than does the climactic type of vegetation. However, they may be just as characteristic as the main type of vegetation, for instance, the peat-bogs in coniferous forest zones, or the mangrove⁷ in tropical rain forest zones.

The following classification will lay emphasis, however, upon the climactic vegetation of each of the sixteen main categories.

(1) *Tropical rain forest.* This is high, dense and evergreen. The trees often develop buttresses or flying buttresses at the lower part of the trunk. They also carry lianas, some of which hang on to the bole while others fall down to form a sort of network. Epiphytes⁸ live on the branches, especially the highest ones. The number of species per unit area is often extremely high, with the result that there is no dominant one. This type of tropical rain forest prevails only in regions where the temperature is very high and varies little during the year, and with an abundant annual rainfall (Amazonia, Malaysia, Congo Basin). Laterization⁹ is the characteristic soil-formation here. In this the alkaline elements and the iron are left on the surface (hence the red colour) and the silica is drawn downwards. The jungle, as it is commonly known, is a secondary forest, which has been altered by man so that the lower tiers are overgrown with bamboos, palms, lianas and bushes. This is different from the primitive forest.

(2) *Temperate rain forest.* The difference between this and the tropical rain forest is in the size of the trees, which are generally smaller, in the very limited number of species, and in the size of the leaves, which are often needle-like. On the other hand, there is more bracken than in the tropical rain forest and there are dense populations of epiphytes, although the number of species is smaller. Mosses can be found, often encircling the trunks like a sheath. The climate is free from frost, although it is cool in winter. The atmospheric humidity is constantly high, because rain and fog are frequent in all seasons. The soil-formation varies between laterization and

podzolization,¹⁰ but both of these are weak. There are real peat-bogs in areas where drainage is difficult. New Zealand, Southern Brazil, Southern Japan and the neighbouring regions of China have vast areas of this forest, but elsewhere it is usually found in islets or belts, and often on the side of a mountain (the Caribbean Islands, Central and Southern Africa, Indonesia, Chile).

(3) *The tropical deciduous forest* loses its leaves for a season. The leaves vary in length. Mostly the trees are stripped of their leaves, but other plants may be affected. There are lianas and epiphytes, and bamboos, whose role is important. This type of vegetation predominates in the hot monsoon countries, where the seasons alternate between excessive rainfall and prolonged drought (eg Burma), and in hot countries with abundant rainfall and a rather short dry season (West Indies). The soil-formation tends towards laterization.

(4) *The temperate¹¹ deciduous forest*: this is dominated by a few species of trees with large leaves which are shed in winter. Herbaceous plants shelter under these trees, and form a carpet in the spring, before the leaves appear. The climate favourable to this formation is temperate, continental and damp; the winters are fairly cold and the summers often extremely hot. The heat partially inhibits podzolization and the soil is brown or grey. Western Europe, the east of North America, and north-eastern China provide examples of this.

(5) *The evergreen coniferous forest* is remarkably homogeneous despite its enormous geographical spread: a few species, or perhaps a single one, such as the spruce in the Alps, predominate. The trees are narrow, cylindrical or pyramidal, and the leaves are very small and dark green. Each species is replaced by another according to the region (Pacific coast conifers, firs, spruces, pines). The forest floor is more uniform; it is mostly covered with mosses interspersed with a few herbaceous plants and shrubs. The circumboreal¹² continental climate, cold and wet, is the one that favours this vegetation, which is rooted in a well podzolized soil, where the drainage permits thorough leaching. Siberia, the north of Canada and equivalent mountainous regions are covered with this uniform acid-loving vegetation. Peat-bogs flourish, for instance, the Canadian 'muskeg',¹³ especially where the drainage has been permanently blocked by recent glaciation.

(6) *The sclerophyllous forest* is low, with trees that have more or less open canopies; the leaves are fairly small, hard and persistent.

There are always a few lianas, often thorny. Herbaceous plants grow abundantly, especially in the spring, but tend to dry up during the summer. The Mediterranean climate (hot-temperate with dry summers and wet winters) produces this type of vegetation, as in Spain, Australia, South Africa, California or Chile. The soil-formation shows a certain fluctuation between laterization and podzolization. Scrub (maquis, garrigue, chaparral, matorral) and steppes are often found on the sites of former forests.

(7) *Parkland*, park-forest or open forest, is not a forest in the sense used here, since trees cover more than 25 per cent but less than 60 per cent of the area. Its structure is variable, as sometimes the leaves are needle-like, such as the yellow pines of California and Nevada, and sometimes larger and leathery, as the eucalyptus of New South Wales. The lower tiers are often very thin, and they usually consist of evergreen bushes and seasonal grasses. The climate is hot and damp enough for the trees to reach full development, but dry enough to prevent them from forming a completely closed layer; it lies between the extremes of tropical rain and drought, but always fluctuates over a considerable temperature range which deviates from moderate conditions. This vegetation may be conditioned by a short-term cycle, rather than by a more or less constant intermediate state. The soils also are not very stable: the drier sites tend towards salinization,¹⁴ the damper to podzolization.

(8) *The savanna* is formed of woody plants, 6 to 30 feet high, covering 10 per cent to 25 per cent of the area. The lower tiers vary widely, ranging from the high Guinean grasses which cover the ground in season, to the crusts of lichens on the banks of the Hudson which are almost as dense, and to the tree thickets¹⁵ of the central African plains. The roots of the plants of the savanna sometimes go deep enough to reach the underground water supply. This sort of vegetation requires a dry season. In hot countries (Central Africa, Brazilian plateau) the drought is caused by the seasonal decrease in rainfall; in cold countries (Siberia) it is the interruption of the cycle by the fall in temperature which stops the trees from growing and spreading. The soils of the savanna are laterized¹⁶ in the tropics, and in some cases they form an impermeable layer at a certain depth. Extreme podzolization in cold countries has the same effect. The tropical savanna is especially prone to fire. Many woody species have a remarkable resistance to burning, but the thick litter of dry

(11) Temperate: ie, of the temperate regions.



Fig. 2. Temperate rain forest at Hagenia, in the Congo.

(12) Circumboreal: surrounding the pole in the North Pole area, between the arctic zone, which is predominantly glacial, and the temperate zone, where the winter is cold but not for very long.

(13) Muskeg: vegetation of the far north of Canada, consisting of basins filled with accumulations of peat.

(14) Salinization: formation of soils of 'salty type'; they are rich in salts, not only sodium chloride but also carbonates, etc.

(15) Tree thickets: clumps of trees covering a smaller area than copses.

(16) Laterized: adjective from laterization (see note 9).

(17) *Caatinga*: type of thorny bush found in Brazil.

(18) *Krummholz*: irregular bush vegetation clipped by the cold winds. Resinous plants, which can reach the size of trees at lower altitudes or latitudes, predominate. Sagebrush: bush of varying thickness, occupying the cold deserts of north-west North America.

(19) *Gleisation*: formation of gley, which is a deep, compact horizon of soils, grey and green as a result of impregnation by iron and manganese in a reduced state.

(20) *Permafrost*: the level at which the soil is permanently frozen and impermeable as a result of the low average temperatures.

(21) *Forbs*: herbaceous plants with wide leaves.

(22) *Tchernoziom*: brown soil. It differs from the *podzols* because the climate, with its long dry season, and the mainly herbaceous natural vegetation do not permit the mineral salts to be leached, so that most of them accumulate in the deep brown soil, rich in humus.

(23) *Horizon*: as used in pedology (science of the soil), it means a stratum or layer as displayed by a vertical section cut in undisturbed soil.

(24) *Desert*: in the strictest sense, a true desert is a region where there is not enough rain each year for herbaceous plants to grow.

(25) *Succulents*: plants with fleshy leaves or stems, such as thick-leaved plants.

savanna, after the end of the rainy season, often goes up in flames.

(9) *Thorny bush* is not more than 25 feet high, and its density varies; it may be more or less impenetrable. The upper tiers of the *caatinga*¹⁷ of north-east Brazil are formed of thorny shrubs and cacti, but the lower vegetation is mostly annual. The equivalent in South Africa has *euphorbias* instead of cacti, but its physiognomy is the same. The climate is desert, except that the drought is interrupted by a short season of heavy rain. The soil-formations are disturbed by this abundant rainfall which causes fairly lateral displacement.

(10) *Scrub* (or bush) also consists mostly of shrubs with a density of over 50 per cent. The Irish heath, the subarctic plantations of alders and *krummholz*¹⁸, the sagebrush of Wyoming and the evergreen beech-groves of Tierra del Fuego furnish examples of where the woody vegetation has very different characteristics. The lower tiers may consist of mosses or herbaceous plants or may not be present at all in regions where the scrub is too thick (coastal bush of Ghana or Angola). The climate is fairly varied, including at least a wet season, if not a constantly high humidity. This type of vegetation seldom covers very extensive geographical areas.

(11) *Tundra* is characterized by low woody plants, which grow in clumps or are bent over near the surface of the ground. Tufts of grass grow amongst these and often clumps or carpets of mosses, and crusts of lichens. Tundra needs a very cold climate, such as that of the Arctic or high mountains. The soil-formation consists primarily of gleisation,¹⁹ which more or less prevents the soil from extending down into the earth, especially in the Arctic where the permafrost²⁰ is close to the surface. The particles of soil are constantly churned by freezing and thawing, so that plant roots break. The heat received and the average temperatures are low; the winds are violent and the season of growth is short. All these factors make for very rigorous plant selection.

(12) *The prairie* is a formation of high grasses in an almost continuous spread. Forbs²¹ often develop and flower late in the season. The prairie always has a long resting period, and its climate is damp continental with a very pronounced dry season. The typical soil is the *tchernoziom*²² with a very thick black upper horizon²³ and calcium deposits accumulated in depth. There used to be a great many spontaneous fires. Herds of herbivorous beasts,

bison in North America and Europe, roamed the prairie in former times.

(13) *The steppe* differs from the prairie in that its grass is shorter and grows in tufts. It is sometimes associated with low scattered shrubs. Annuals grow on the bare spaces for short seasons. The continental climate of intermediate latitudes is favourable to the steppe, especially where the dry season is preceded by winter rains. The soil is drier than that of the prairie and so there is no deep black layer even on the best sites, but a characteristic brown horizon instead. Excessively drained soils lend themselves to the accumulation of alkaline elements. The steppe is often grazed and cultivated, with cereals and cotton, for example; in many places, such as Dakota and Asia Minor, the exploitation has been followed by severe erosion due to rain and wind, with consequent sand- and mud-storms.

(14) *Alpine grassland* is a formation of short grasses, tufted, green and very often interspersed with mosses, which predominate in places, and more scattered woody plants. The climate is more alpine than arctic. In the mountains low temperatures are often compensated by high day temperatures in the summer, as the mountain ranges share the general climatic conditions of the region.

(15) *Desert*.²⁴ The chief characteristic is the scarcity of the vegetation, although the hot deserts (Arizona, Sahara) always have a great number of annual species. These are often minute and do not always appear every year. Otherwise, there are trees, succulents,²⁵ shrubs and herbaceous plants which occupy up to 10 per cent of the area. These plants have developed many ways of saving water, for instance by succulence, reduced leaf surface, or wide dispersion of the roots. The climate is characterized by extreme drought because of the lack of precipitation. The temperature is generally higher than in the tropical rain forests, and its range is distinctly continental. The soil-formation tends towards salinization, that is to the accumulation of alkaline elements near the surface where salt deposits may be formed.

(16) *The crust*. The only areas where the crust predominates are at the extreme limits of vegetation and particularly on rocky substrates, for example, in Greenland and the Sahara. In such cases, it is exclusively composed of cryptogams—lichens particularly, but also algae and mosses. It is not more than a few inches thick.

These descriptions of the main plant landscapes of the world bring out only the more striking features of the primitive vegetation.

Domestication of plants



A grain of wheat: symbol of the contribution of plant life to man's well-being. (Photo Lod).

Hybridization



Fig. 1. Hybridization is one of the commonest methods used by the horticulturist to obtain new species—attractive to the eye, and often resistant to parasites and diseases as well. Here is a typical example of the technique which has been used to create a new variety of iris. Dr M. Simonet (National Institute of Agricultural Research, Versailles) has used the pollen from *Iris aurea* (top left) to fertilize a flower of *Iris Carthaginiensis* (bottom left) to produce a hybrid (above) retaining the striae of the mother plant, but with coloration from both parents. (Photo Lod).

From wild to cultivated plants

Roger de VILMORIN

The countryside—its physical character, its plants and animals which are readily recognized—gives an illusion of permanence in nature. Nevertheless we must appreciate that throughout geological time the earth has undergone many modifications which have affected the geographical distribution of plants; moreover, plants have a capacity for variation, which is expressed by slow but continuous changes.

Mutations,¹ brought to the fore at the beginning of research in genetics, are constantly occurring among wild plants; and we now know how to produce them experimentally by means of various physical and chemical agents. In nature, these mutations are the result of the fortuitous action of the environment, of heat, cold and various radiations causing hereditary modifications within the cells.

Within the same species plants carrying these new characters have the ability to hybridize, that is to cross with each other, and so increase the variation more or less indefinitely. Some of the new sub-species produced by disadvantageous mutations, have been eliminated by competition. On the other hand, others, more vigorous and better adapted to a different ecological environment, have flourished locally or even spread and invaded other territories. Mutations are able to affect not only the morphological characters of a plant, such as the colour and size of the flowers, the height of the plant and the shape of its leaves, but also the physiological characters—resistance to cold or to disease, for example; and one can readily understand how these sub-species, with mutations, have established themselves in situations where the

parent species could not succeed. Hybridization also fairly frequently produces unusual varieties, of which many examples are known, particularly among the graminaceae (especially maize) and tobacco plants.

Primitive man had before him an extensive plant kingdom which was undergoing intense intraspecific variation; he was able to choose the best species for his own use and amongst them the best hereditary types.

Before the beginnings of agriculture, during the nomadic period, our ancestors were limited to gathering wild plants and letting their flocks wander and feed where they could. Gradually, man began to work the soil, planting bulbs and tubers and sowing grain. By the end of the neolithic period man had become, in fact, an agriculturalist, thus marking one of the most important stages in the evolution of plant life from the wild to the cultivated state.²

Yet another stage in this process of development, and no less important, was geographical in essence. Most of our cultivated plants have come from afar, having travelled by natural dissemination and, above all, by the route of human migrations; and later, by acclimatization, that is to say by systematic introduction and cultivation (fig. 1).



Fig. 2. The chief centres of origin of cultivated plants (Darlington and Vavilov): (1) eastern and central China (2) India (3) Indonesia and Malaysia (4) central Asia (5) the Near East, Iran (6) Mediterranean basin (7) Abyssinia (8) central America (9) north-west region of South America (10) eastern region of South America.

(1) A mutation is an alteration in a gene or chromosome which shows itself by an immediate change in a hereditary character. Fluctuation, on the other hand, is an expression of the non-hereditary differences which are always observed among individuals of the same species.

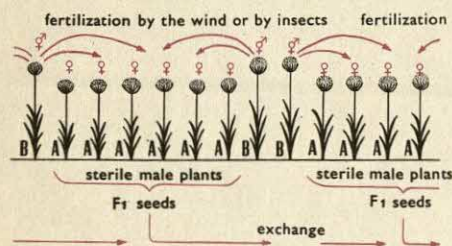


Fig. 3. A diagram showing how seeds of the F1 generation can be produced in a plant with hermaphrodite flowers, by making use of male sterility (onion).

(2) 'Biology acquires its full significance only when considered as an historical science, for life is laden with the past'. (Albert Vandel).

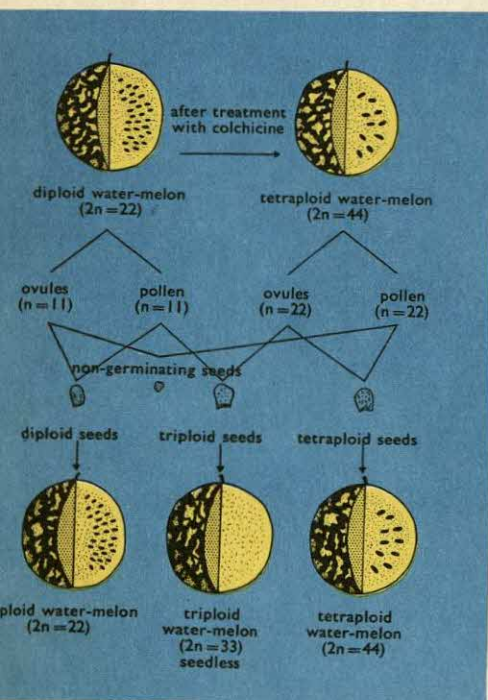


Fig. 4. Experimental polyploidy in the water-melon.

Man's intervention was at first quite empirical, but became less so as knowledge advanced. This had two important effects—first, the process of variation was intensified and speeded up; second, selection became anthropocentric in character. Man selected from chance variations not the types most advantageous for the future of the species itself, but those which lent themselves to the purposes he had in mind. He was (and he is) thus able to produce monstrosities: cauliflowers with enormous heads,³ abnormal artichokes, savoys and Brussels sprouts, flowers in which the sex organs are partially or totally transformed to become largely ornamental, and melons, grapes and tomatoes without seeds, all sterile.

In sum, man, forced by the need to obtain food, could not be satisfied with the small and slow variations of nature; he learned to multiply and accelerate them to his own advantage—at first empirically, and then by design, so that wild plants have become transformed into cultivated ones with profoundly different hereditary features.

Methods of improvement

For our purpose, it is best to exclude the period before the seventeenth century. Lacking sufficient knowledge, our remote ancestors were able to do little more than preserve their endowment of vegetation, increase this by chance introductions from foreign journeys, and perhaps isolate the fortuitous mutants or hybrids with valuable features. The information we now possess is sufficient to make us realize that, until quite recently, edible vegetables and decorative plants were little different from wild ones. Improvements in plants, essentially conditioned by sexuality, were scientifically impossible before fundamental knowledge of the science of botany—especially of the mechanisms of fertilization—had been discovered. Following this, improvements in plants took place in two stages: pre-genetic, during the nineteenth century, and the genetic stage, beginning in 1900.

The pre-genetic phase

At the beginning of the last century many great minds studied methodically the ways of improving plants. Vast collections of plants came into existence and these increased as the world was more thoroughly explored. Systematic hybridization became a commonly practised procedure; it was soon discovered that

the first generation after crossing was composed of plants which resembled the parents and were intermediate between them. In contrast, it was noted that the second generation produced many different forms; some resembled their parents, whilst others were distinguished by the possession of new characteristics. Thus the science of selection was born, or more precisely, the method of genealogical selection, which is concerned with the sources of systematic crossings, and, in particular, the isolation from the second generation onwards of families and lines with comparable features, of which only the best are preserved. First introduced by Louis de Vilmorin, this method has produced many new and useful plants, some of which are of considerable economic importance, such as sugar beet with a high sugar content, and wheat with a very high yield. Kitchen vegetables and ornamental plants have benefited from the same methods, so that the number of varieties has increased immensely. We now have, for instance, long or short carrots with tender hearts; early, part-early or late savoys; cauliflowers and broccoli at all seasons; and many varieties of petunia, chrysanthemum, aster. Indeed, nearly all the vegetables which we eat and the flowers grown in our gardens are the result of careful selection.

Those who carried out selection in the 'pre-genetic' era were well aware of the fundamental differences in the sexual behaviour of the different genera of plants on which they were working. They were able to distinguish between autogamous plants fertilized by their own pollen, which produce pure strains in some generations (corn, wall-flower, lettuce, etc); and allogamous cross-fertilized plants, which are fertilized by the pollen of sister plants. For these plants selection results in a homogeneous population, but not in a pure line,⁴ (beet, rye, spinach, etc). In addition many transitional types between the two extremes were noted. These early research workers also observed the vigour of hybrid plants and were aware of the many peculiarities of sexual biology, which they soon learned to exploit in order to help perfect the production of cultivated plants in day-to-day use.

From the first quarter of the last century, plant selection was carried on with a view to influencing not only the physical characters of plants, but also their chemical and physiological functions, for example, the amount of dry matter in chicory or the early maturity of many vegetables. In reality, and this is a

strange and important historical fact, applied genetics⁵ was being practised before genes themselves had been discovered. In other words, when Mendel's laws—the fundamental principles relating to the transmission of hereditary characters—were rediscovered and published in 1900,⁶ they were to explain only the results that had already been methodically obtained throughout the century; though, of course, they made genealogical selection more rapid and economical, in reducing notably the effects of chance. Later, the science of genetics developed with staggering complexity and opened up new horizons completely unsuspected in the 'pre-genetic' era.

It is these new horizons which we shall now discuss.

Applied genetics

The fundamental contribution of the laws of genetics has been to teach us how to investigate the hereditary characters of living organisms. Cytology, and more particularly nuclear studies (karyology),⁷ have demonstrated that these factors are contained in the chromosomes of the cells. It is now realized that the cytoplasm is also involved in the hereditary mechanisms, and that the chromosomes and the genes which these mechanisms contain are susceptible to modification by different agents, sometimes producing mutations which are beneficial to man. Moreover, a better knowledge of the hereditary character of floral biology has opened up new possibilities in plant propagation. It has appeared that the classical diagrams of the morphology and physiology of the sex organs are not fixed like a series of uniform structures, but that there are, on the contrary, a large number of particular cases: plants normally hermaphrodite, but accidentally and hereditarily deprived of one or other sex; partial or total sterility, auto-incompatibility, as a result of which plants are fertile with pollen of other plants but not with their own; polyploidy; and other valuable anomalies that have already been exploited profitably.

One may say that the methods which each day separate cultivated plants more clearly from their primitive ancestors⁸ come under the heading of diversity. Varied techniques have been introduced for selectively cultivating plants according to the nature of the subjects and their floral pattern; the exploitation of mutations; research on resistance to parasites; the utilization of hybrid-vigour; male sterility; experimental polyploidy; ex-

polyploidy; exploitation of one sex; parthenocarpy; the use of X-rays, gamma rays, neutrons and other radiations.

Types of selection

There are about ten methods of selection, which differ according to whether the plants are perennials, biennials or annuals; and the type of pollination—whether autogamous (self-fertilized) or allogamous (cross-fertilized).

We may exclude the simple methods of vegetative reproduction whereby plants multiply by means of suckers, runners, tubers, rhizomes and bulbs. These are clones which, once obtained, always resemble each other indefinitely; examples are roses, irises, strawberries, and potatoes. These clones are, however, often used as the starting point for the creation of new varieties. By self-fertilization, or coupling, or by crossing several individuals with each other (polycross), it is possible to obtain a number of different strains. If some of these new varieties show advantageous features, it is usual to go back to the parent plants, increase these vegetatively and then make the original cross on a large scale. This is a very

(3) The enormous heads of certain cabbages are really hypertrophied buds, and without human intervention these plants could not survive. The same is true of the double-flowered wall-flower, which is totally sterile. There are many similar examples amongst cultivated plants.

(4) A pure line is a collection of identical individuals, whose characters do not vary in subsequent generations except for environmental modifications.

(5) Genetics: see the volume entitled 'The Living Organism', which contains a chapter on 'Problems of heredity'.

Fig. 5. A rose nursery. Greater knowledge of the hereditary characters of flowers has opened up entirely new horizons in horticulture. (Photo Lod).



(6) *The fundamental laws of genetics were discovered by Mendel in 1865, but the original publication was ignored until the facts were rediscovered and published in 1900.*

(7) *Cytology is concerned with the structure and function of cells; karyology is the study of the cell nucleus.*

(8) *'When we compare the individuals of the same variety or sub-variety of our older cultivated plants, one of the first points which strikes us is that they generally differ more from each other than do the individuals of any one species in a state of nature' (Charles Darwin).*

(9) *In the first, or F_1 , generation resulting from a cross between forms in which a certain character*

Continued on next page

new technique and has been used with fodder graminaceae to produce improved clones which are much superior to the wild varieties found on the prairies.

Without attempting to describe all the methods of selection, two which are in current use may be mentioned.

(a) Selection of annual plants which are normally self-fertile; for example, wheat, barley, oats, peas, beans, tomatoes, ground-nuts, tobacco plants. Suppose that we wish to improve wheat by uniting in one plant two characters held by different individuals, such as a good yield and resistance to black rust. After the cross has been accomplished we select from the heterogeneous population of the second generation (F_2) those plants which show the desired characters, and we then follow their descendants for seven or eight generations, eliminating the defective types and preserving only the best. These are propagated by self-fertilization and so tend to produce strains which are genetically pure

(homozygotes).⁹ When they are followed and observed in their separate lines they are carefully compared with each other to see which strains come closest to the ideal required. This plan is simple in appearance but is really much more complicated when the selection involves, as is almost always the case, not just two but a large number of characters.

(b) Selection of cross-fertilized plants which produce seed only once and are assessed before they flower.¹⁰ Examples of these among edible vegetables include cabbages, of which we eat the heads; beets, turnips and radishes, the roots of which are eaten, and onions, of which the bulb is the edible part. These species are self-sterile, and so it is not a question of obtaining pure strains as in the selection of wheat, but of homozygous populations for the greatest number of important characters. One starts with a population from which all the defective individuals are eliminated; the remainder are allowed to mature and seed, either all together or in pairs. The next generation is tested and only the best descendants are preserved; thus a number of strains are obtained which differ from each other and from the original population. If they have desirable qualities, they are retained as new varieties.

There are other and more complicated methods of selection; for instance, for cross-fertilized plants whose usefulness cannot be determined until after they have flowered (maize, gherkins); for cross-fertilized plants which are susceptible to vegetative propagation (rye), and for those many perennial species which produce seed several times throughout their life and are spread by means of seedlings. Moreover, there are certain plants which have a peculiarity in their make-up and cannot be fitted into any of these schemes. One can thus gain some idea of the complexity of methods of selection.

Exploitation of mutants

Mutations which occur spontaneously in nature (for example, the appearance of white flowers in a species which is normally coloured) are still utilized in selection, but only in a subsidiary way,¹¹ for we now know how to stimulate the production of mutations by means of X-rays and other radiations. These radiations, which are usually directed against the nuclei of the cells, nearly always cause damage to the tissues and may destroy them; the plants that survive, as a rule, show regressive features.¹² The number of novelties of any

Fig. 6. From wild to cultivated wheat. Left: an allopolyploid from *Triticum persicum* and *Aegilops squarrosa* which grows naturally in Georgia. Centre: a soft variety of wheat grown in the Middle Ages and which is still cultivated in remote parts of France. Right: a soft variety of wheat which is the result of modern selection. (Central Station of Plant Selection. Photo Lod).



value obtained by this method is limited, but nevertheless this field of improvement will probably increase. The application of methods using neutrons, gamma rays and other radiations is becoming more precise and accurate all the time, so that we are leaving the realms of pure research and are beginning to make practical use of them. There is no doubt that in the near future we may expect a great deal from nuclear research in the service of plant biology.¹³

In the field of research into the resistance of plants against such enemies as insects, fungus and virus diseases, natural mutants have already shown their value; it is sufficient to preserve the individual carriers of resistant genes. Yet absolute resistance is encountered very rarely, and the search is more for resistant genes amongst wild species. In this way, for example, genes resistant to nematode (round worm) infestation and septoriosiis in tomatoes, discovered in two wild American species, have been used in applied genetics.

Experience has shown that the hybrids (F₁) obtained from a good cross are often superior to the parent plants. This hybrid-vigour, or heterosis, which was first established on an experimental basis by Darwin, is reduced rapidly during subsequent generations, together with the heterozygous characters. Heterosis after crossing shows itself not only in the vigour of the plants, but sometimes also by the introduction of other interesting qualities such as precocity, or resistance to disease and to parasites, and the plant grower often takes advantage of this peculiarity.

If the species can be propagated vegetatively there is no real problem, for the plants of the first generation can be multiplied by cuttings, in the manner of a clone,¹⁴ and hybrid-vigour is conserved indefinitely as in poplars, which nowadays usually outclass their parent forms.

When the chosen species bears hermaphrodite self-fertilized flowers it is only necessary to remove the stamens from one plant; the emasculated 'mother' plant is then fertilized with pollen from another ('father') plant. In this way it has been possible, for example, to obtain a number of tomatoes and artichokes which combine vigour with good yield and precocity.

If a species that is hermaphrodite and self-sterile is being worked on, it is necessary to isolate lines that are totally self-sterile, for crossing experiments. It is of course unnecessary to remove the anthers from these plants.



Fig. 7. Possible mode of origin of soft varieties of wheat. *Triticum persicum* which is still cultivated in Georgia. Centre: the weed, *Aegilops squarrosa*, which grows with it. The hybrid of these (right) with a doubling of chromosomes—allopolyploidy—grows naturally in Georgia: it could be the starting point for soft varieties of wheat. (Central Station of Plant Selection, N.I.A.R., Versailles. Photo Lod).

The selection of cabbages is a good example of this particular method. It is best to repeat the cross each year so as not to lose the benefits of heterosis.

Finally, heterosis is readily exploited amongst monoecious plants, that is, those which have separate male and female flowers on the same individual plant (cucumbers). This is also true of dioecious species such as spinach in which some plants are entirely male and others entirely female. In the first case it is simple to remove all the male flowers from a plant chosen as 'mother' and to fertilize the female flowers with pollen from another plant. In the second case the male and female plants are grown side by side so that cross-fertilization takes place.

Although these techniques cannot be employed with all cultivated species, the exploitation of heterosis is one of the most promising and spectacular features of genetics.

But there are other methods, no less ingenious, among which the use of male sterility is of prime importance. In many species certain individuals bear sterile stamens; and these plants, although morphologically hermaphrodite, are functionally female—a

Continued from previous page
is dominant and another recessive, only dominant characters appear; but in the next generation, or F₂, recessive or masked characters appear in a known proportion. For example, if a green pea is crossed with a yellow one all the plants in the F₁ generation produce yellow peas, since the yellow character is dominant. But the next generation, F₂, contains 25 per cent of plants which have green peas; when these recessives are crossed with each other they breed true and give plants which yield only green peas. These are known as homozygotes, for they are genetically pure for the character of seed 'colour'.

(10) Cross-fertilized plants cannot be bred in pure lines by artificial pollination, for there is frequently a genetic incompatibility between the male and female sex organs of the same plant. Moreover, inbreeding tends to produce defective characters in certain plants, just as in animals and human beings.

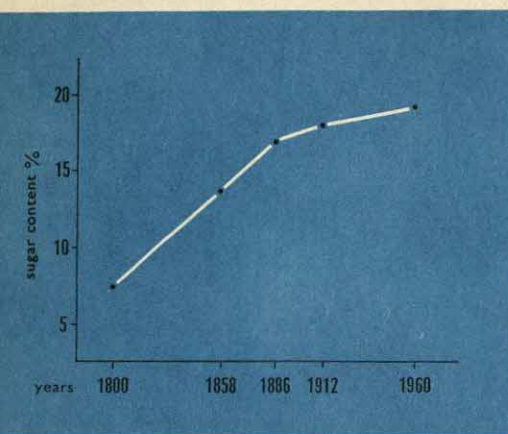


Fig. 8. Graph showing the increase in sugar content of sugar beet over the years.

(11) 'A mutation gives us the impression of a mistake in development, a "printer's error", frequently absurd, sometimes innocent, but very rarely advantageous.' (Jean Rostand).

(12) The transformation of sexual organs in ornamental specimens may involve complete sterility; this apparent absurdity is an advantage in the cultivated plant, but would obviously lead to extinction of the wild plant.

(13) See the next chapter, 'Atomic radiation and crop improvement'.

(14) A clone is simply a plant which is first grown from seed and then multiplied indefinitely by vegetative reproduction without involving any sexual mechanisms. Examples are: potatoes, fruit trees, strawberries, garlic, rose trees and perennial plants. This particular method of growth and reproduction sometimes occurs naturally.

(15) The number of chromosomes is fixed for a given species but is extremely variable according to the species. For example: $2n = 6$ in *Crepis*, 24 in the lily, 64 in the dahlia.

(16) Like male sterility, parthenocarpy, heterosis and polyploidy are not man's inventions, for all these are found among wild plants. But credit is due to the scientists and growers who discovered these phenomena and have learned how to exploit and sometimes induce them experimentally.

characteristic which is hereditary. Hence, hybrids of the first generation can be produced without any difficulty, because the use of sterile males does away with costly and delicate castration procedures. This method was first tried out in the United States, using the onion: in this castration is practically impossible because the stamens are so small. Male sterility has also been discovered in other species—notably the tomato, from which several excellent hybrid varieties (F₁) have been obtained. Moreover, male sterility in some species of beet and carrot is being selected at present. This is therefore an anomaly which, associated with heterosis, has assumed considerable economic importance (fig. 3).

Experimental polyploidy

During cell division the chromatin filament, which is the essential part of the nucleus, breaks up into spherical or cylindrical bodies—the chromosomes—of which there is a fixed number in each species.¹⁵

From the researches of Morgan and his school we know that the chromosomes carry the hereditary factors and transmit them from generation to generation according to Mendel's laws of segregation, and by a variety of mechanisms which have since been discovered, in particular by Darlington. The number of chromosomes in each cell— $2n$, or the diploid number—is halved to the haploid number (n) in the reproductive cells of the pollen and the ovule, so that when the cells fuse to form a new individual the diploid number appropriate to the particular species is reconstituted.

When certain substances, notably colchicine, are applied in specific concentrations and under certain conditions to various plants, the number of chromosomes may be doubled to $4n$ (this effect, which is also dependent on the species used, can be produced by action on the seeds of the plant or on the organs during growth). Plants in which the normal diploid $2n$ has become $4n$ are known as autotetraploids (polyploids) and are of considerable scientific and practical interest. The polyploid state is always accompanied by changes in the physical characters of the plant which are of some interest in selection. The stems of the plants are often taller, more rigid and less branched than in the diploid variety; the leaves are larger, always thicker and of a darker green; the floral peduncles and pedicels are longer and thicker, and the flowers bigger, with stronger colours; the pollen grains and seeds are larger, and generally the fruits.

Though these modifications are not always favourable to agricultural and horticultural improvements, some of them are extremely beneficial, such as the increase in the size of flowers and of the intensity of their coloration. A large number of tetraploid plants have already replaced their diploid ancestors, and this fertile source is far from being exhausted.¹⁶ Yet these benefits of experimental polyploidy are not confined to the growing of flowers. Many varieties of sugar beet, for example, have an industrial importance far superior to the diploid strains, and it is now possible to cultivate several plants and vegetables (rye, clover and various kitchen vegetables) and get an increased yield.

When a diploid hybrid obtained by crossing two species, doubles its chromosomes, the result is called an allopolyploid, which has its own characters, is fertile, and breeds true. It is through allopolyploidy that varieties of wheat have probably evolved from wild species (fig. 7). A triploid can be obtained by crossing a diploid with a tetraploid plant, and the chromosome formula is $3n$. These odd-number polyploids are always sterile, which is a disadvantage to the plant, but useful to the grower, because in this way seedless fruits such as water-melons and grapes (fig. 4) can be produced.

From experience we know that male and female dioecious plants do not always behave in exactly the same fashion. Certain characters are known to be sex-linked in their inheritance, and many examples can be found amongst plants, animals and human beings. So if a valuable sex-linked character is discovered the grower is tempted to produce only that particular sex. For instance, the male plant of the asparagus is approximately 25 per cent heavier than the female. Moreover, the male is more precocious and has a longer life-span. It is really remarkable that by means of applied genetics it is possible to produce colonies of asparagus plants which are males only.

A final phenomenon is parthenocarpy—the ability of some plants to produce fruits without fertilization: bananas, grapes, tomatoes and cucumbers. As this phenomenon is influenced by genetic factors, it will be used by the geneticist in future to produce a large number of edible fruits and vegetables.

This is a brief outline of the techniques at the disposal of the plant grower. More and more discoveries may be expected as we improve our knowledge of the functions of the nucleus and cytoplasm of living cells.

Atomic radiation and crop improvement

Seymour SHAPIRO

From the biologist's viewpoint, one of the most important properties of atomic radiation is its ability to induce *mutations*, which can be defined as sudden structural or chemical alterations in the hereditary material which is located in the nucleus of the cell. Such changes are of great interest to the geneticist and plant grower. The former is interested in mutations because they represent a drastic disturbance in the orderly mechanism of inheritance; the latter because occasional, naturally occurring mutations impart new characters of economic importance. When it became apparent that atomic radiation could very considerably increase the rate of production of mutations, both groups of scientists eagerly seized upon this new research tool.

The first significant indication that one could experimentally increase the mutation rate came in the late 1920s from the experiments of H. J. Müller and L. J. Stadler, working independently with fruit flies and barley, respectively. They discovered that after exposing their material to X-rays, there was a substantial increase in the frequency with which certain characters were mutated to a different form.

How does radiation produce a mutation? The determining factors of heredity, called *genes*, are organized on, and constitute a part of, certain discrete structures, called *chromo-*

somes,¹ which are within the nucleus of every cell of all plants and animals. In order to change the pattern of inheritance, one must alter these genes or their arrangement on the chromosomes. Radiation, whether it be light, heat, or any of the various types of atomic radiation, is a form of energy, and energy is capable of performing work. All of the atomic radiations are also called *ionizing radiations* because, either directly or indirectly, they produce charged atoms, called *ions*, as they pass through matter. When energy, in the form of ionizing radiation, is beamed through tissue, some of it will strike the chromosomes of the nucleus of one or more of the cells. In traversing the chromosome some of the energy is absorbed and this may result in a structural change in the molecules of which the chromosomes and genes are constituted. Small alterations which may not be accompanied by any microscopically detectable changes may, however, be the cause of obvious changes in the growth and behaviour of the plant. Such changes are called *point mutations*. Often, however, the amount of energy absorbed is sufficient to break the chromosomes and the broken pieces can be clearly seen upon microscopic examination. Changes of this magnitude are called *chromosome aberrations*. Broken chromosomes may re-join. Often several different chromosomes in the same cell may



Fig. 1. Irradiation of peach trees with radioactive cobalt has brought about varied physiological transformations. In particular, certain of the trees treated have produced branches of which the fruit ripens a week earlier than in the initial variety. An example is this branch of the variety 'Fairhaven', shown here alongside a branch of the normal variety. (Photo Brookhaven National Laboratory, U.S.A.).

(1) Genes and chromosomes: see the volume *'The Living Organism'*—the chapters entitled *'From cell to tissues'* and *'Problems of heredity'*.



Fig. 2. Among the mutations induced by radiation is that of flecks of pale pink appearing in the rose variety *'Better Times'*. (Photo Brookhaven National Laboratory, U.S.A.).

(2) The research that has served as the basis for this chapter was carried out at the Brookhaven National Laboratory (U.S.A.) under the United States Atomic Energy Commission.

break and re-joining of the broken ends may take place in combinations that are quite different from the original. Thus a broken end of one chromosome may become joined to a broken piece of a second chromosome, and so on.

It should now be clear that when a mutation takes place it occurs in a single cell. This cell generally must divide a large number of times to produce enough tissue for the mutation to be recognized and used. Mutations which occur in cells that are not destined to divide further are almost never detected and are certainly of no practical use. If the plant is propagated by seed, the tissue derived from the mutated cell must extend into the flower and reproductive structures and finally into the seed if it is to be detected and used. In plants propagated asexually by cuttings, the altered tissue must reach into a bud from which it can then be propagated and increased. Thus, only a few seeds or a few buds first display the mutation. For this reason, the new type will generally appear as one branch, all or part of which is distinctly different from the rest of the branch and the remainder of the plant. From this initial appearance of the 'sport' one must propagate a large enough population to permit a critical evaluation of the new type.

The greatest part of this newly created variability will be deleterious, and sterility is common. However, if one has specific objectives of improvement in mind and can employ accurate and efficient means of screening large populations so as to reveal the presence of rare individuals carrying the desired traits, then the sacrifice of large numbers of plants is of no great consequence.

In addition to its mutagenic properties just discussed, radiation may produce beneficial changes of a permanent sort by a quite different mechanism. Most plants possess the same genes in all of their cells. However, despite the fact that all cells generally carry the same genes, the expression of a gene is dependent upon the location in the plant of the cell that carries it. Thus, although root cells contain the same genes for flower colour that are present in the cells of the petal, only colour genes present in the cells of the petal have an opportunity to control the colour of the flower.

In the course of some radiation experiments with the *Sim* group of carnations, Y. Sagawa and G. A. L. Mehlquist, working at the Brookhaven National Laboratory and the University of Connecticut, discovered

that when plants of the variety *White Sim* were irradiated with an appropriate dose of x-rays or gamma rays, some 60 per cent of the irradiated branches produced red flowers rather than the usual white. In a similar fashion, irradiated *Pink Sim* plants also produced large numbers of red-flowering branches. These red-flowering branches appeared in every respect to be identical with a third *Sim* variety, *William Sim*, and it was known that both *White Sim* and *Pink Sim* had originated as spontaneous sports of *William Sim*. Breeding tests revealed that both *White Sim* and *Pink Sim* were chimeras and contained an internal core of tissue with genes for red flower colour (*William Sim*). However, presumably by spontaneous mutation in one of the outer cell layers at some earlier time, these cells were now overlaid by tissue with genes for the expression of white or pink flower colour. As colour in the carnation flower is located only in the outermost cell layer of the petal, only cells in that position were able to express their colour genes. Thus the conversion of the red-white (*White Sim*) and red-pink (*Pink Sim*) chimeras into red-flowering plants must somehow have permitted the core cells with red flower colour genes to reach the surface and gain expression.

What are the accomplishments thus far of the radiation approach to plant growing? In horticultural plants a number of new and interesting types have been produced. At Rutgers University, L. F. Hough and his colleagues have been studying the effects of radiation on peach trees. Sports for both earlier and later ripening fruit have been found as single branches, or parts of branches, on irradiated trees of the varieties *Fairhaven* and *Elberta* (fig. 1). Some of the peach mutations have also resulted in firmer fruit flesh and changes in fruit texture. In the variety *Brackett* a sport was discovered from the normal freestone to the clingstone pit condition. Horticulturists at other institutions have reported fruit colour changes in apples and pears; a larger fruited muscadine; and disease-resistant currants.

In the field of floriculture, G. A. L. Mehlquist has selected several improved carnations from his radiation experiments and these are now being evaluated under commercial growing conditions to determine their overall suitability for release as new varieties. These selections include changes in colour, flower form and increased vigour of the plants. Flower colour changes, largely because of the ease with which they can be detected, have

Fig. 3. Irradiation of comparatively tall plants: a powerful source of gamma rays, 2,000 curies of radioactive cobalt-60, is put in the centre of a kind of amphitheatre, on the tiers of which are arranged the plants to be treated (tobacco, bilberry, peach, etc). As the intensity of the radiation received varies according to the distance from the source, each plant can be exposed to the requisite dose by being moved nearer to or farther from the centre. (Photo Brookhaven National Laboratory, U.S.A.).

been found in a large variety of species, among them *Saintpaulia*, cyclamen, phlox, snapdragon, tulip, rose (fig. 2), chrysanthemum, geranium and petunia.

As work was started earlier with agronomic plants than with horticultural ones, the status of research with agronomic species has progressed further. At least seven new varieties have been released to the markets of the world as a consequence of experiments in radiation. Four of these new varieties were developed and released in Sweden, the country first to initiate such studies on an extensive level. These radiation-produced varieties are the *Primex* fodder pea, *Regina II* summer rape, the *Weibull Stralart* fodder plant, and *Palace* barley. A new bean, called *Schafers Universal*, has been produced in Germany, and the *Sanilac* kidney-bean and the *NC4X* peanut are the results of efforts in the United States. In addition to those already on the market, a much larger number of potentially useful mutations are undergoing extensive testing and evaluation which will determine whether they are directly useful, useful when incorporated into other existing varieties, or of no value because of concomitant deleterious features from which the useful trait cannot be separated. Radiation-induced characters at this stage in development include dwarf forms of rice, sorghum and barley with little or no accompanying loss of yield (but which render the plants less susceptible to wind damage); more robust stalks and a deferred ripening time in a whole range of graminaceae, disease resistance in wheat, oats, flax, groundnuts, barley and blue-grass; and increased yield in several different species.²

When one considers the relative infancy of research in this field, the long period required for testing selected mutations and sports, and the large number of still unanswered theoretical questions, the answers to which will undoubtedly increase the efficiency with which radiation is used, the results at this point seem highly encouraging.



The cultivation of plants with or without soil

Pierre CHOUARD

The cultivation of plants is nothing other than the whole of agriculture. This book, however, is not intended to be an agricultural encyclopedia; nevertheless, it is necessary to explain in a few words the relationship between plant life and agriculture, for it is the most important of the relationships between the vegetable kingdom and man.

The earliest revolution in agriculture was the association of animal rearing—a source of supply of manure and fertilizers—with the cultivation of plants and vegetables. This type of agriculture, which lasted in antiquity and throughout the Middle Ages, was developed quite empirically. The second great change began with the Renaissance and flourished in the nineteenth century; it was founded on the rationalization of methods of cultivation analyzed and interpreted in the light of planned scientific experiments. That was the agriculture developed chiefly to supply the needs of the peoples of the western hemisphere at the same time as they pioneered the world of science and technology. Because of that agriculture it became possible to support an ever increasing population, in spite of the fact that at the same time more and more people were being employed in expanding industries.

Agriculture can also be regarded as a way of life, that of the peasant who lives and works close to the soil. With scientific progress he has become an agriculturist or farmer, and having developed technical skills, he takes his place in the modern world alongside the industrial worker.

The progress of modern agriculture is an impressive spectacle. In Europe at the beginning of the nineteenth century wheat yielded hardly 4 to 5 cwt an acre even in good soil; sugar beet contained no more than 6 per cent sugar; maize was cultivated in very few areas and was of such poor quality that it was used only for feeding fowls; and the potato was subject to epidemic diseases like that which ravaged Ireland in 1841, causing the loss of two million people, who either emigrated or died of famine. Today, a little more than a century later, wheat yields about 20

cwt to the acre, sugar beet contains 18 or even 20 per cent sugar, maize is grown nearly all over Europe and yields approximately 30 cwt an acre, and the potatoes which are now grown are resistant to the most dangerous diseases.

How was this progress accomplished and how is the basis of future agriculture being laid?

A plant is to be regarded as a machine which receives energy in order to transform raw materials into essential substances. Energy is obtained from the sun; the raw materials are water, carbon dioxide, oxygen and certain minerals which are dissolved in the moisture of the soil. This machine is not man-made. It is itself alive, reproduces itself, and can be said to possess its own qualities—good and bad. Man's function is to analyze the mechanisms of plant life, and the conditions which affect its functioning, favourably or otherwise, and to study how to interfere in its very reproduction so as to select good qualities and eliminate the bad ones, as far as possible.

Agriculture as a science

Broadly speaking, there are four main lines of scientific progress in the development of agriculture—nutrition, genetics, pathology, and developmental physiology.

The physiology of plant nutrition is the equivalent, scientifically, of the use of fertilizers and manure in practical agriculture. The main themes have already been outlined in the earlier chapters of this book. At first it was believed that plants are able to gain food from rich earth, for instance, from manure. Later, at the end of the eighteenth century, it was discovered that water and carbon dioxide in the air were essential to plants; and that they

were utilized as a result of the action of sunlight on chlorophyll, though the details of this astonishing reaction were not understood for another hundred and fifty years. At the same time the essential role of oxygen for respiration and of water in internal processes was appreciated. But plant nutrition could not be maintained by these elements alone. Liebig, in Germany, and Boussaingault, in France, about 1840, established the necessity and fundamental role of certain substances normally found in fertile soils. These are substances which are responsible for the fertilizing power of manures: nitrogenous salts (nitrates and salts of ammonia), potassium salts, phosphates, sulphates, and salts of calcium and magnesium. After 1870 the equally fundamental importance of trace elements began to be appreciated; these include iron, copper, boron, zinc, manganese, cobalt, molybdenum, iodine, chlorine, etc. Very soon were discovered the function of soil bacteria and the important part they play in manufacturing nitrogenous substances and thus supplying essentials for plant nutrition.

The effect of these discoveries on the cultivation of plants is obvious; as a result we can explain many traditional agricultural practices, which have undoubtedly benefited from the new knowledge gained.

In practice we are unable to control certain factors which influence the growth of plants, such as the amount of sunshine, rainfall, the content of oxygen and carbon dioxide in the air, the temperature (except in special shelters or in glasshouses) and the general climate, which favour or hinder agriculture. But, with care, it is possible to modify other factors of the environment with advantage. Breaking up the soil facilitates the aeration of the roots; the action of bacteria enriches the soil with compounds of nitrogen taken from the air; manure provides some minerals in diluted form and these organic materials which are essential for the activity of bacteria in improving soil fertility; and the colloids of the soil (loam and humus) help to conserve mineral ions (such as ammonium, potassium and phosphate) for the use of the root systems, chiefly by preventing their being washed away by the rain. It is also possible to enrich poor soils by adding mineral elements, particularly those most often needed—nitrates, phosphates and potassium symbolized as N, P, K.

If fertilizers are added at the right time, the composition of the soil can be regulated to counteract the impoverishment which results from successive crops. By this means we do away with the method of laying land fallow,

which was the practice in the past, when as part of the system of crop rotation some land was left fallow to allow it to improve by bacterial activity and the slow attack on insoluble minerals in the soil. The soil can be analyzed and the requirements for fertilizers estimated, season by season, without interrupting the sequence of cultivation.

Moreover, the rotation of crops can be arranged so that plants sown in succession are complementary to each other. Leguminous plants, for example, are used to enrich the soil with nitrogen; they are able to do this through the action of root bacteria.

In tropical areas primitive methods of agriculture led to impoverishment of the soil, for deforestation and the heat of the sun rapidly turn the land into desert; but by employing modern scientific methods these destructive influences can be overcome. It is also possible to increase the humus in the soil by the addition of compost, combined with nitrogenous fertilizers which make good the loss of nitrogen by bacteria in converting compost into humus. The vital importance of water has been learned, the necessity to reduce assimilation at the approach of hay-time, and the introduction of irrigation to supplement insufficient rainfall.

It has even become possible to use carbon dioxide, 'gaseous manure', although it proved very difficult at first. It is now widely employed in the mass culture of aquatic algae, although

Fig. 1. Cultivation without soil, in the Sahara. The sand (from the Erg) is placed in a forcing frame. Pipes, pierced with small holes, are embedded in the sand and carry water enriched with mineral fertilizers. The irrigation fluid never reaches the surface of the sand and thus losses due to evaporation are kept down to a minimum; the water is conserved for the transpiration needs of the plants.





we do not know how to keep it in contact with the foliage of aerial plants.

Fields of technical progress

Genetics—the physiology of heredity—is the scientific name for the selection and improvement of plants.

Physiopathology is the counterpart to the maintenance of plant health. It is the study of the relations of plants to their disease agents such as fungi, bacteria, viruses and insects. There have been many triumphs in the application of this particular branch of knowledge, and in some instances it has been possible to double productivity or even save a whole harvest from total destruction. Notable examples are the victories over diseases due to phyloxera—a fungus which attacks grapes and also potatoes—and the scourges of the potato beetle, cereal rusts, ‘black spot’ of fruit trees and the ‘sereh’ of sugar-cane.

The physiology of growth and development is the most recent line of progress in scientific agriculture. By its means we are able to accelerate growth by curtailing dormancy as in lilac and lily-of-the-valley; we know about the factors regulating growth, such as auxins which afford improved propagation by cuttings; and we can force plants, such as pineapple, to flower regularly. Weeds can be selectively destroyed when they are growing in the midst of cultivated plants. Further, we have begun to unravel the mysteries of physiological effects of the seasons, vernalization, photoperiodism, thermoperiodism, and to use them in cultivation.

Another line of progress is technical rather than physiological, namely the extensive mechanization and motorization of agricultural work. Machines are used widely in cultivation, in the treatment of plants for pests and diseases and in the many and varied processes of harvesting and carrying. Manual labour is reduced to a minimum and many of the hardships of work done away with; essential operations can be completed in the required time. This revolution has enabled agriculture to come within the economic pattern of the modern world.

Fig. 2. The radish and lettuce shown here have never been in contact with soil. The seeds were placed on glass wool and covered with ‘Vermiculite’ (expanded mica), these two substances acting as support rather than nutritive media. Since the perfusing fluid contains mineral salts, the seeds have germinated and grown into vegetables of the finest quality. (Produced in the phytotron at Gif-sur-Yvette. Experiment by Nitsch. Photo Lod).

Culture without soil: hydroponics

We have already indicated the chief functions of the soil in relation to plant life. It acts as supporting material for the roots, which carry the stems and foliage; it is a reservoir of water and of nutritious salts; it provides a supply of slowly liberated insoluble elements, and is the site of extensive bacterial activity which serves to manufacture nitrogenous materials and helps to liberate elements in reserve and manufacture humus. This in turn is important in the utilization of fertilizers, and is a factor in stimulating and inhibiting many processes in soil physiology that are not yet fully understood.

But fertile soils are unequally distributed throughout the world, and the question arises whether it is possible to cultivate plants without soil. Here are some of the processes that have been used in attempting this type of cultivation.

In the middle of the nineteenth century physiologists developed the idea of rearing plants by growing them with their roots in solutions of various nutritious substances or in inert siliceous gravel perfused by these solutions. The object of this method was to seek out the materials and elements essential to plants; and this was done by varying the composition of the nutrient fluids and observing the effect on growth, the so-called 'synthetic method' of investigation. Without its being realized, the technique of cultivation without soil had been founded.

But it was not until 1936 that these processes were actually developed on a large scale for use in agriculture and horticulture, chiefly at the instigation of Gericke in the United States. Unfortunately the press seized on the early reports and stated, quite erroneously, that cultivation in synthetic media would soon replace the use of fertile soils. As a reaction to these exaggerated statements all interest in these techniques was disclaimed, just as falsely. The truth lay somewhere between the two extreme viewpoints.

The method consists essentially in making basic preparations of mineral salts which are diluted so as to form the final solutions in which the plants are grown. The dilution is made with fresh water containing no more than a trace of calcium (which would precipitate the phosphates), and with a reaction that is slightly acid ($\text{pH} = 6.0$ to 6.5). The medium must also contain all the necessary elements—N, P, K, S, Ca, Mg, in sufficient quantities (a total amount of the order of 0.7 to 2.5 grams per litre) as well as the trace

elements—Fe, B, Cu, Zn, Mn, etc., in a proportion about 100 to 1,000 times less; and all the constituents must be in suitable proportions and in well-defined equilibrium.

There are different methods of using the cultures.

Culture in water: the roots sink into the liquid and the plants are held up by supports above the container; the stems pass through holes in plates which keep the solutions in the dark and thus prevent the growth of algae; a trellis-work almost flush with the surface of the water helps to support small plants. The solution must be aerated and, like perfusion fluids in physiology, can be continuously renewed, changed or periodically enriched. Some plants which have good food reserves can, at certain phases of their development, be grown in pure water for short periods, as one does with hyacinths in a vase of water. Water cress, a plant with minimum requirements for minerals, is usually grown in beds: a very old method of cultivation in water.

Culture on sand or gravel: the roots of the plants are grown in a solid supporting medium which is porous and chemically inert, such as coarse sand, silicate gravels, ground-up bricks, well-washed clinkers, glass wool, or even granules made of plastic material. The same perfusing solutions are used as described above, but there are many ways of distributing them to the plants: intermittent or continuous irrigation from above (drop by drop), slow percolation of the sand or gravel with fluid which is sometimes recovered and used again, or continuous irrigation from below with solutions which are forced up through the depths of the medium without ever reaching the surface. The methods vary, but the simplest is to bury plastic pipes, with small holes in their sides, in the sand. These artificial methods of cultivation may be compared with the natural cultivation of flowers in parts of Holland, where near Haarlem, flowers are planted in the infertile sand of the polders with a rich supply of fertilizers, above a constant level of fresh water.

The different types of cultivation without soil have been given the name 'hydroponics', because they are based on the use of water and various solutions, in contrast to the standard agricultural practice of tilling the soil, which is sometimes called 'geoponics'.

One of the major difficulties in using hydroponics as a method of growing plants is that, in the absence of the colloids of a true soil (clay and humus), the plants have nothing in reserve for active feeding; they are at the

Fig. 3 (right-hand page). For many years to come, the majority of crops will assume the same aspect of profusion presented by this field of maize; less rational, perhaps, than artificial cultivation without soil, but more pleasant to look at. (Photo Lod).

mercy of any operational accident, such as a breakdown in the irrigating system or an error in the composition of the solutions. On the other hand the method can always be used in areas where there is not enough fertile or fertilizable soil; and provided the climate is suitable (whether natural or modified artificially, as in a greenhouse) the plants can prosper. In fact the yield and quality are at least as good as those obtained naturally from well-fertilized soil. The cost of production is naturally higher, and so the use of hydroponics is more or less restricted to growing certain vegetables, flowers and, occasionally, fruits, especially in parts of the world where these products would otherwise have to be imported at great cost.

Apart from its commercial use, hydroponic cultivation is an interesting and instructive way of growing plants in the home, and it also has numerous applications in the laboratory in connection with scientific research.

The greatest significance of this method of cultivation lies in its use in arid climates. For example, recent experiments in the Sahara

have been carried out using only sand (of the siliceous type from the Erg) irrigated from below through plastic pipes in large vats. Large yields of vegetables have been obtained in all seasons with very little water: only one-third to one-tenth of the amount required in the oases for the same crops. The chief limiting factors in agriculture in dry climates are the lack of naturally fertile soil and, above all, the lack of fresh water. By using hydroponics for cultivation in these countries, the natural cultivation factors are completed, and then with the wonderful supply of sunshine and good daily temperature conditions, the circumstances for vegetation are found (paradoxically) to be truly the best. Since water will always be costly in the Sahara and in other desert regions, hydroponic cultivation will make for considerable economies.

Of all the practical applications of plant physiology in the technical sphere, this new science of hydroponics, together with the mass cultivation of algae in fresh water, constitute the greatest agricultural advances in the war against world famine.

Mass culture of algae

Hiroshi TAMIYA

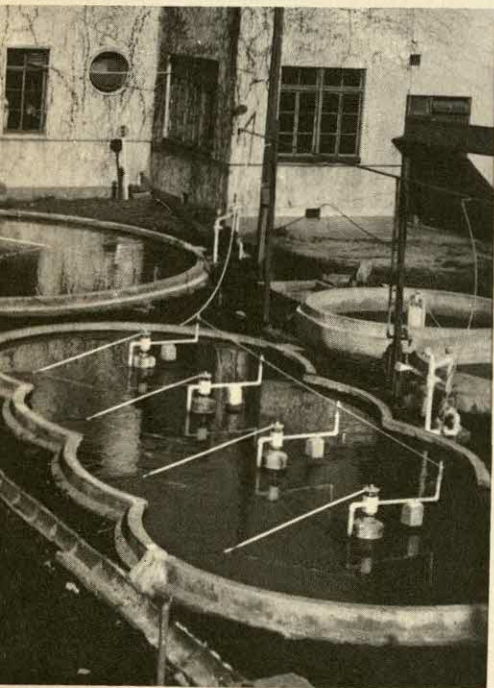


Fig. 1. Culture ponds operated in Japan for the growth, on an industrial scale, of Chlorella.

The yield of crop plants grown by conventional agriculture is, at the most, 2-5 tons total dry organic matter per acre per year. Laboratory experiments performed by plant physiologists have indicated that a considerably higher yield, as much as 40 tons dry weight per acre per year, would be obtainable if we were to grow tiny aquatic algae, such as *Chlorella* and *Scenedesmus*, under adequately controlled conditions. Various attempts have been made to grow these algae in mass on an industrial scale, since they are found to consist of material of good nutritional value for human beings and animals. They contain on a dry weight basis approximately 50 per cent of protein, 20 per cent each of carbohydrate and lipid and 10 per cent of minerals, besides various important vitamins.

For the active growth of the algae, besides light, carbon dioxide and mineral nutrients the culture needs continuous or occasional agitation. This has a dual purpose: it distributes carbon dioxide and nutrient substances evenly in the culture, and it prevents the precipitation of algal cells. To realize these conditions in outdoor cultures,

culture ponds, as shown in the picture, were constructed in Japan, and were operated throughout the year in order to test the feasibility of algae-farming. The yield was found to fluctuate according to the season and was lowest in winter and highest in summer. The average yield was 8.6 grams (dry weight) per square metre per day, which would correspond to a yield of 13 tons per acre per year. This is equivalent to the production of 14,000 pounds of protein per acre per year: a yield which is considerably higher than that obtained in the cultivation of ordinary crops, which gives some 200-600 pounds of protein per acre per year, or in raising cows to obtain milk and meat, which produces only 50-90 pounds of protein per acre per year.

Before such algae-farming can become commercially feasible, however, two problems remain to be solved: first, how to construct and operate culture ponds on a large scale economically and efficiently; and second, how to process the harvested algae so as to make them palatable to people who are unaccustomed to their taste.



Man and the world of plants

Jacques ROUSSEAU

Man with his delicate and relatively hairless skin is one of the most vulnerable of all the mammals to the inclemency of the weather. But at first the fur and wool of animals were inaccessible to him. So was silk, the weaving of which required a certain refinement. The true plant textiles, the weaving of cotton tufts, the fibres of hemp, of flax and of china-grass imply an advanced state of civilization or, at least, a summary agriculture. On the contrary, other fibrous substances do not need elaborate preparations: for example, the strips of bark of the Western Red Cedar⁽¹⁾ with which the Red Indians wrapped their babies, the tufts of the Graminaceae, the beaten bark of Polynesian waist-cloths, or the woven leaves of rudimentary clothing. Mat and basket weaving preceded the art of textiles.

Footwear, which is indispensable in certain countries, appeared first in the form of the sandal. As this requires less pliability than other forms, it was natural to choose less flexible fibrous plants. Nowadays artificial silk or rayon, derived from wood, has for the most part supplanted natural silk. Plastic fibres, ultimately derived from 'fossil' oils of vegetable origin are being substituted for wool and furs.

Where clothing is concerned, the only mineral contribution is asbestos, which is used for special fire-proof uniforms; houses, on the other hand, are largely dependent on it. However, it was once necessary in many regions to make do with vegetable products. The fronds of palm trees were used for tropical huts; the semi-settled fishermen of British Columbia made their dwellings of planks because they had timber (*Thuja plicata*) which was easily split with primitive tools; the native of eastern Canada used birch bark for his house. If he had to emigrate, the house was dismantled in less than thirty minutes and he would set off with the walls rolled up.

Birch bark was used likewise in the making of canoes, and it is this material which

opened up the forests of northern Canada to discovery and civilization. Without tools to cut a route through the undergrowth and without draught animals, the Red Indian forest dweller could still travel easily during the winter with snow-shoes and on toboggan. On the other hand, the impossibility of hunting game in summer in the inextricable undergrowth would have reduced him to famine were it not that river and lake had given him a route suitable for his canoe. Thanks to his alliance with the birch, the Algonquin was able to anchor himself in the most ancient continent in the world and develop there an autochthonous form of culture. Only a canoe made of bark can be dragged from one lake to another on the track trodden by moccasins.

The most primitive means of transport depend on the vegetable world, whether those means be a raft of reeds or bamboo, a canoe formed from hollowed tree-trunks, a long-boat of planks, a sleigh, a litter, a push-cart, a carriage, skis or snow-shoes. The Eskimo's kayak, made of seal-skin, generally includes a framework of wood or, rarely, of bone; the canoe made of moose-skin (the Canadian elk), used in the Rocky Mountains and formerly in eastern Canada, has a wooden framework and is derived from the bark canoe; the boats, round as drums and, made of the skins of bovines (oxen, bison, buffaloes), which are found in various parts of the world (the Palestinian region, and formerly in the Canadian prairies), also included wood. The Eskimo sleigh, occasionally made from whale-bone, but more frequently from flotsam, slid on runners made smooth by a coating of liquid mud polished with a cloth.

Those indispensable auxiliaries of food and shelter—fuel and lighting—are everywhere derived from the vegetable kingdom, except by some maritime hunters who use the oil of sea mammals, and others who use fish oil; among shepherds the dung of herbivorous animals is used for the same purposes.

(1) The Western Red Cedar tree, *Thuja plicata*, is not of the same genus as the Cedar of Lebanon, *Cedrus Libani*.

It was scarcely some centuries ago that wood as a means of heating was supplemented by coal (massed petrified vegetation), gas (a by-product of coal) and one of the forces of nature, electricity.

Plants, the medium of thought

Man may be defined as a gregarious, sociable animal. After uncontrolled gesticulation and inarticulate cries, words appeared, which made the subtlety of his thoughts more and more clear. But speech is fleeting and demands the presence of other speakers. In order to communicate from a distance man invented writing. Here again plants formed the medium. The Indians of north-east America used the signs of tracks of which scouts made use. A mark made with an axe on a tree-trunk indicated which direction to follow. A felled tree placed obliquely at the entrance to a path, either with the branches at its head removed or not, with or without stakes in a line, indicated the halting places of the hunter, his chances of food supplies, his state of health, or any accidents that had happened and the urgency of the help required. When descriptive hieroglyphics succeeded phonograms which indicated sounds, simple plant shapes were sometimes chosen to illustrate them. The runes of Ogam,² on the other hand, are composed of twenty-five more or less arbitrary signs corresponding to the names of twenty-five different trees whose first letter gives the phonetic value to the rune.

Except for the use of vellum, parchment, silk and stone, writing is based on materials of vegetable origin. The birch bark of north-east America, the pounded leaves of trees in eastern Asia and elsewhere, have been used as vehicles for thought. In Egypt the papyrus was cut up into strips which, when woven together and subjected to pressure, gave a thin sheet of great strength. Eventually, paper made of a paste of vegetable fibres appeared. It is perhaps not inappropriate to mention that the word *folio*, like the French word *feuille* (sheet of paper) is derived from *folium*, which denotes the leaf of a tree, and that *livre* (book) is derived from the Latin *liber*, which at first denoted the fibrous sheets of the inner side of the bark or bast of certain trees. (Strictly speaking, this tissue belongs to a vegetable structure which is still called *liber*; before the invention of papyrus, *liber* would even have been used for writing; in the poplar, especially, this is made up of broad sheets.)

The most popular ink in Europe was



Fig. 1. Man cannot live by bread alone, but without bread he could not live. (Photo Lod).

made down the ages from the gall-nut. Instead of using goose quills, the Chinese wrote with brushes made from wood, which had a strong influence on the style of their ideograms. The cuneiform script of Asia Minor likewise owes its style to the instrument used for writing. Marks were made in the clay by pressing it lightly with the end of a piece of reed, which was tapered, bevelled, and thicker on one side than the other, thus giving it strength. The imprint had the outline of a forged nail or of a wedge, whence the name of the writing.

Plants play a part in every form of human activity. Basket-making and primitive dyeing were dependent on them, as were rubber, and the oils and resins of paints and varnishes. In ancient times perfume-making was based entirely on plants. They were indispensable, too, for utensils, tools and arms. Arrowheads, knives and axes were made of flint, obsidian

(2) Runes: letters of the old Scandinavian alphabet.

or quartz; but the arrow, the bow, the handle of the axe or of the javelin, the club, the hoe and the dart could not be made without wood.

Rites of religion and recreation

What is an essential part of human life cannot but find its place in religion. Numerous religious ceremonies are accompanied by incense-burning. Myrrh, as well as other balsamic and aromatic substances, and also pitch, were used to embalm the dead before their journey to the hereafter.

Palm Sunday sees brought into honour the date palm of the Mediterranean region; other palm trees, notably in America; the willow covered with catkins, among the Slavs; the branches of thuja, formerly used in French Canada; the bay-laurel, which was then called the rose-bay, in lower Normandy; and branches of box in the region of Paris—and it is still with box that one sprinkles the dead when they are laid out.

Sometimes a plant may become an object of veneration or curses, as in the case of magic herbs used in philtres. The ancient Canadians spoke of the 'scattering plant' (*Coodyera repens*), an orchid which was reputed to lead astray those who crushed it under foot. The folklore

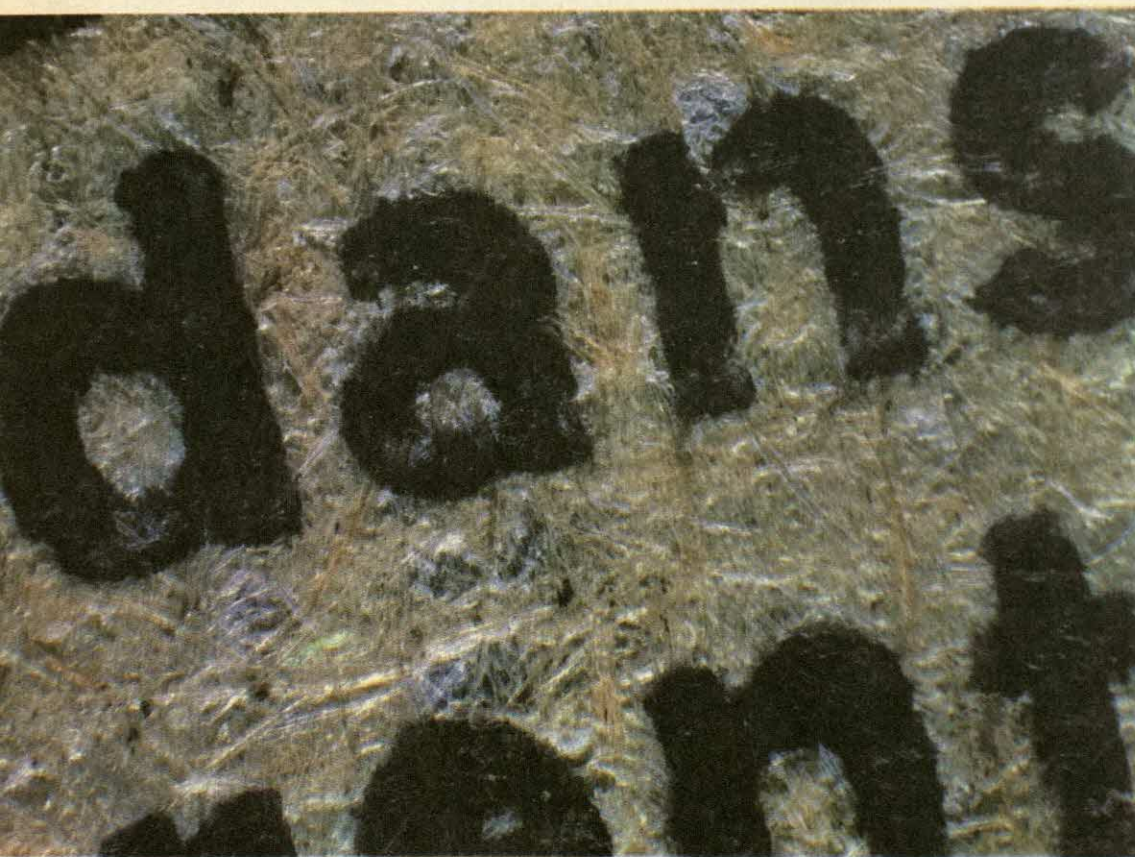
of all countries is rich in descriptions of plants as bearers of doom or of blessings. In Britain youths used to pass under the mistletoe during the Christmas festivities, thus perpetuating a rite which can be traced back to their Celtic past. This plant, sacred to the Druids, was distributed on New Year's day, from which rose the folklore expression: 'The New Year is the mistletoe's'; an evergreen, it symbolized the immortality of the soul. In some African religions the baobab tree (*Adansonia digitata*) has the significance of a spirit. The voodoo of Haiti has transferred this veneration to a related tree, known as 'kapotier'. In Palestine, a plant known as the Apple of Sodom (*Calotropis procera*), an Asclepiad, bears a dry fruit with the external appearance of an apple; in local tradition it is an accursed apple tree. In the oasis of Dakhla in Nubia, on the seventh day after birth, a child is placed on a sieve with a pinch of salt and a handful of corn, barley and rice. As soon as the mother shakes the sieve, the grains fall to the ground; they are then flung north, south, east and west to bring luck to the child and to protect him in the course of his journeys.

It is natural that man should organize rituals in honour of gods who protect cultivated plants. The Romans venerated Ceres. Indian peasants attended elaborate ceremonies at the time of seed-sowing, germination, ripening and harvesting. In one such ceremony, the women ruffled their hair frantically, as a symbol of silks vibrating in the wind. Species whose domestic cultivation is lost in pre-history take their places in this pantheon. Among the Iroquois Indians, the Three Sisters, maize, the gourd and the bean, personify real spirits. The Sioux, having become nomad hunters and abandoned agriculture in order to hunt bison, continued to venerate maize.

In Mediterranean rituals an offering of smoke was made by burning incense on embers and Red Indian fire-worshippers inhaled the smoke from bunches of slow-burning vegetable matter. It appears, in fact, that this custom of smoking was at first a religious act before it became profane. Many plants were used besides tobacco, which alone has kept its hold. The Red Indians were engaged in trade before the arrival of white men and produce was sent not only from the Atlantic coast to the centre of the Continent, but also from the Arctic Sea to the Pacific coast and from the Gulf of Mexico to the valley of the St Lawrence.

It was not long before the natives became acquainted with cigars, cigarettes and a variety

Fig. 2. Plants are the carriers of the written word, thought and information. This fragment of a newspaper, magnified under the microscope, reveals its vegetable origin and structure. (Photo Lod).



of pipes, one of which had two tubes that were inserted in the nostrils. The use of opium and other drugs, especially those causing hallucinations, sometimes fulfilled a religious function; sometimes it was merely a diversion. It was through religion above all that plants became associated with the decorative arts. The acanthus, the lotus and the papyrus flourished on Greek and Egyptian capitals. The floral motif found its apogee in the Gothic cathedral.

The tree and nature's protection

It remains for us now to consider the function of plant formations independently of their content. A forest resembles a great canopy protecting the soil against direct action by the sun. When sunlight is filtered weakly through the foliage it does not dry up the fallen leaves: their debris is turned slowly into humus which acts like a sponge. This layer prevents the trickling of water through the soil, and soil erosion.

In the temperate zone, the ground is normally covered with a carpet of continuous vegetation. In order to introduce agriculture, this carpet must be worked and harrowed, only the plants of the furrows being allowed to remain. Rain lays the soil open to leaching, and on a steep slope fertile soil gives place to arid sand. This is sometimes sufficient to turn large fertile areas into deserts.

The bare mountains of Haiti were formerly covered with valuable woods, but planters felled the trees in order to settle on the slopes; terraces were missing, and thus in the rainy season there was nothing to prevent the torrential rains from washing the soil away to the sea. A photograph taken in India shows what appears to be a tall tower, but it is actually the masonry of a well exposed by erosion. In the Arizona deserts, a rain-storm lasting no more than an hour will hollow out a water course thirteen feet deep because there is no vegetation to protect the surface; whereas in the province of Quebec patches of forest provide bulwarks against erosion.

Forests exercise a regulative influence on the temperature which should not be underestimated. The foliage prevents the drying out of the soil where, during the day, lower temperatures are experienced than in the fields. During the night the protecting screen of foliage prevents the loss of heat by radiation. Frosts are not caused by cold coming down to the ground, but because air which has been warmed through contact with the soil rises into the atmosphere. Low clouds act as a mantle and foliage plays the same role.



Fig. 3. Plants are indispensable to man for his protection from the weather. Here, highly magnified, is the west of linen. (Photo Lod).

Trees in regions of low rainfall draw water from considerable depth and give it forth in the atmosphere. This humid air helps to improve climatic conditions. The problem does not arise in western Canada, where there is abundant water; but the forests, through their litter of leaves, retain the water from precipitation and regularize the flow of the rivers, thus averting summer drought.

Forest land harbours insectivorous birds, which benefit cultivated land, as well as fur-bearing animals and game. Things of the least economic importance often contribute to the pleasure of life: the song of birds; the sight of a timid partridge or hare; the sudden leap of a buck; the eland browsing on the water lilies of lakes; the hard-working beaver felling a trembling poplar with its sharp teeth—what more does one need to create 'theatre' of the most varied kind?

Plants and salubrity

Forests must give way partly in order to make room for the development of agriculture, and, in a more radical way, for towns.

By means of photosynthesis, plants assimilate the carbon dioxide in the atmosphere. At night, of course, this function remains in abeyance; plants, like animals, require to break down organic matter by giving off carbon dioxide, the reverse function, thus, of assimilation.

An increased number of trees in a city augments its supply of oxygen. The air, tainted by smoke from factories and houses,

is perhaps vitiated even more by the increasing number of cars. It was noticed that the paulownia flowered poorly in Paris during the years which preceded the war, but during the occupation, of 1941-4, when because of the shortage of petrol there ceased to be any traffic, it flowered well. During the summer of 1960 the chestnut trees in Paris wasted away in spite of a rainy season which normally suits them: their poisoning was attributed to leakage of gas and the incomplete combustion of car petrol. Professor Roland Portères has observed that damage of this kind is less when the trees are close to strong artificial light: it appears that the unusual chlorophyll activity caused by street lighting lessens the danger of their being poisoned.

The plant kingdom and civilization

There is in existence a botanic weft in the history of the world. The vine was introduced into Gaul twenty centuries ago by the Romans and, with wheat, shaped the country's agricultural future. In 1492, Columbus searched the West for the kingdom of spices and precious timber. When Jacques Cartier lay up for the winter in Quebec in 1535, part of his crew was saved from scurvy by the thuya. During the same period, Europe turned to the West Indies for the cultivation of the sugar cane: this produced the slave traffic, and indirectly the ostentatiousness of Versailles. Cotton in the United States required the introduction of cheap labour. Whitney's invention of the cotton gin, more than the Declaration of the Rights of Man, ended American slavery.

Eastern Canada was drawing the larger portion of her income from furs when Napoleon's Continental blockade deprived England of Baltic timber essential for her fleet. Britain, thus obliged to look elsewhere, turned to her new colony. Great conifers were felled and floated down to the sea as serried rafts, so making possible the industrial expansion of Canada.

Man is not content to tolerate his environment; he struggles with it and modifies it. He not only creates the microclimate of his dwelling, but sometimes transforms nature, with irreversible results. Fire and the impoverishment of the soil gave rise to the maquis of the Mediterranean region, as we know it, to the thorn-bush maquis of the Iroquois, and also to the desert. Increases in population create a need for new dwelling places, and this need has to be met by such

expedients as the reclamation of polders from the sea and agricultural clearings which have to be protected from the encroachment of forests. The French colonist in New France tries to reconstitute the marshes of Poitou or the copses of Normandy. Everywhere a procession of weeds follows in man's footsteps, insinuating themselves into the new associations of plant life and sometimes destroying them.

Seed-sowing, harvesting and milling necessitate a permanent dwelling place. Stability protects the inhabitants, if there is agglomeration. The farmer, unlike the hunter, wants neighbours.

Cultivation increases edible matter at will and populations grow. When the Germanic tribes lived on game and scavenging, about $3\frac{1}{2}$ square miles were required to feed one individual. Today in France about 4 acres are sufficient. The Red Indians of the United States and Canada probably did not exceed more than a million. The same region now has a population of over 150 millions.

The diversity of florae leads in its turn to differences in cultivation. The Gramineae of the steppes influence the type of living differently from the conifers of the temperate regions, or the agaves of the desert regions.

Species cultivated in different parts of the world require different agricultural methods, different ways of life, and consequently a ritual proper to each. Wheat, rice and corn, three important cereals, are the foundations of the three principal civilizations of the world: the Mediterranean region, centre of the civilization based on wheat and bread; the Asiatic centre, from which the civilization based on rice spread; and the American region, which was the centre of the maize civilization. Of less importance are the civilizations based on sorghum in Africa, the taro in Polynesia, the manioc of the Caribbeans, the tef in Ethiopia, the yam in Africa, and the millets of eastern Asia.

Who invented agriculture? The nameless numbers of neolithic men, labouring like beasts of burden and crushed by the monotony of their lives? The beaver gnaws ceaselessly, and when he has felled trees with the incessant action of his teeth, he has accomplished an engineer's task and saved his species. Who has measured the ripples of a sheet of water? Yet the waves which erode the shores of continents imperceptibly create new continents; and it is through the spilling of grains of corn around the cooking-pot that womankind has invented agriculture.



Fig. 4. Whether used as building material for boats or for houses, wood is one of our most precious aids. (Photo Lod).

Plants and industry

André FAURE

During the thousands of years which preceded the Industrial Revolution, the vegetable kingdom provided the necessities of life almost exclusively, either directly or through the raising of crops, and hunting. This situation has, however, altered considerably, and many of our contemporaries react against any dependency of industry on an agricultural origin as being a survival from times that are spent.

Man relied on the vegetable kingdom to produce, apart from his food, cloth and clothes, furniture, dyes, varnish, cleaning material, drugs, and the means of heating; later, he drew on it for the energy requirements of the early iron industry, for the beginnings of constructional work and vehicle manufacture, and for his means of transport—herbivorous * animals. * Perhaps only stone quarries and metal-producing mines were excepted from a direct or indirect agricultural origin. The handicrafts of yesterday were thus largely dependent on the vegetable world.

If man has given in to the temptation to do without natural products and to make use of artificial substitutes, it is without doubt because of a long period of development which has lasted since the middle of the eighteenth century. When, for example, a large international firm considers it utopian to base an industry on agricultural products, one feels that it reflects a fear of uncertainty mixed with the pride of the sorcerer's apprentice.

One must bear in mind, unfortunately, that while great industrial concerns are tempted to dispense with agricultural products, they destroy natural resources and devote fabulous sums to their research, out of proportion to what the improvement and selection of natural products would cost.

In order to demonstrate the advantage of the use of the vegetable kingdom in industry, we shall cite three examples: petroleum and coal, textiles, and new industrial openings for agriculture.

Petroleum, coal and textiles

It is scarcely disputed nowadays that deposits of coal, however uncertain their formation may be, appear to be the result of anaerobic fermentation working on the remains of plants once exposed to solar radiation.

It seems that the origin of petroleum is due to a similar action on animal and vegetable remains, as in the case of numerous oolite and carboniferous deposits. Thus directly or through the intermediary of the animal

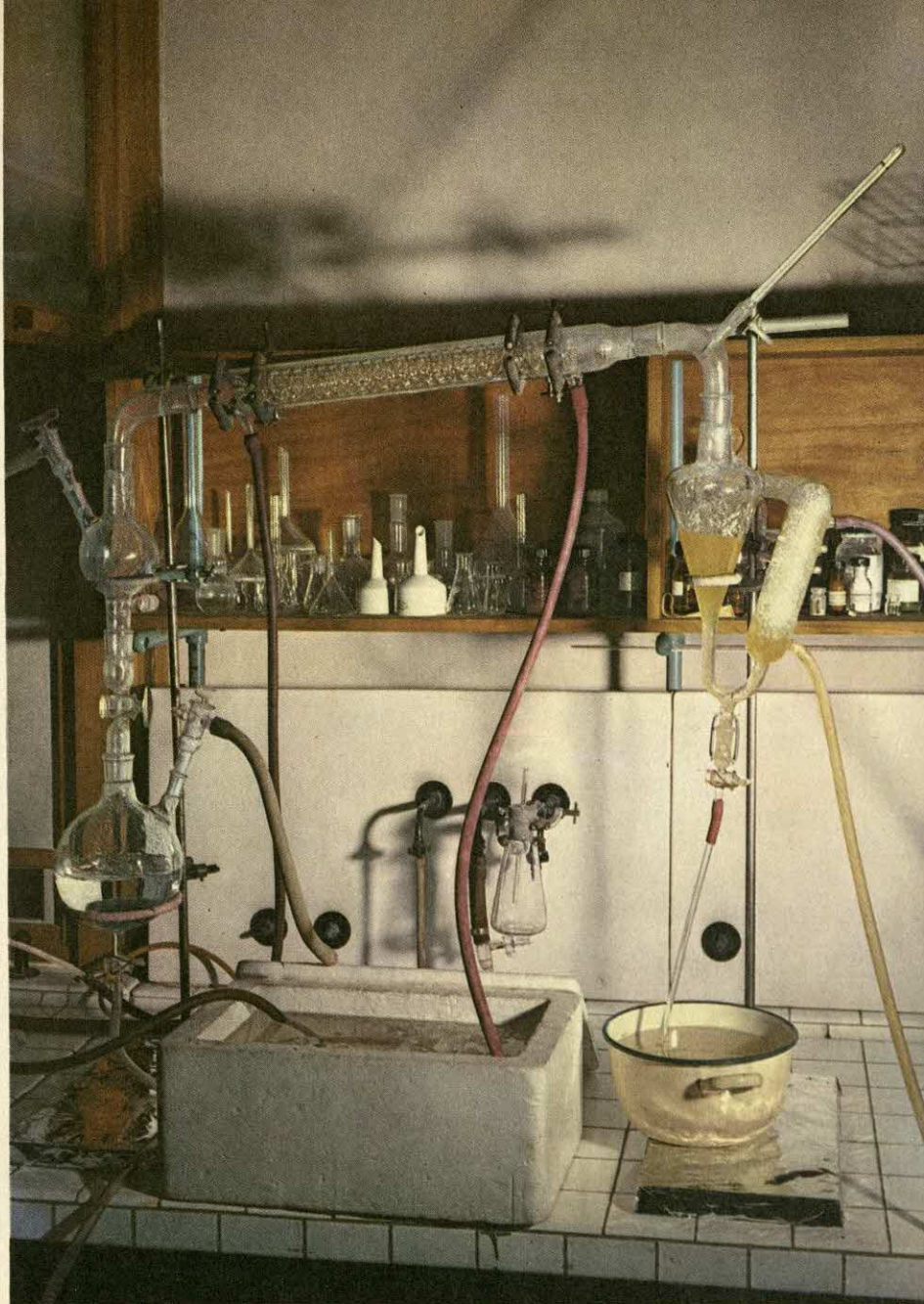


Fig. 1. A plant is an almost inexhaustible source of organic products, which it synthesizes much more neatly than does the chemist. In fact a whole branch of chemistry is busy isolating compounds made by plants. We see here one phase in the extraction of a hormone of cellular division, contained in the cambium layer of the poplar. The yellow extract (on the right) is sucked into a flask and slightly heated by means of a helicoidal tube through which warm water is flowing. The solvent is retrieved through condensation under low pressure. (Photo Lod).

(1) Teilhard de Chardin: 'The Future of Mankind'.

kingdom, the origins of petroleum and coal are linked with the vegetable kingdom.

It is easy to realise that plants form the potential source of carbonaceous and other compounds. These latter supply rich material for the chemistry of oil and coal.

Fifty years ago, the use of plant textiles was limited to the cultivation of hemp, cotton and flax. The processing of these fibres was difficult and costly. The steeping of flax was a laborious process, and all that exertion produced a thread which, without belittling its good qualities, was coarse compared with the synthetic threads we know. In the meantime, the vegetable kingdom has found a new importance through 'rilsan', which is manufactured not from synthetic material but from castor-oil. This latter contains 85 per cent of triricinoleate of glycerine, which, after a

variety of processes (cracking), gives a molecule of 18 carbon atoms. This, when divided, is broken into a molecule of 11 carbon atoms (undecylenic acid, which is the useful fraction) while the 7 remaining carbon atoms form a straight chain aldehyde.

Specialists declare that rilsan has qualities characteristic of, and in certain respects preferable to, those of other fibres. It is only proper to mention that the Americans do not deny that the only practical way of correcting the defects of artificial fibres is to mix them with natural fibres.

The future of chemurgy

We define chemurgy as the sum of activities whose object is research into new outlets making use of equally new processes of industrial transformation of the products of agriculture, and particularly the surplus by-products of industries concerned with agriculture and nutrition.

We can distinguish two fields:

(1) *Heavy chemurgy*, which consists of making use of solar energy and thus permits man to utilize the carbon which he needs, has every chance of lasting as long as life. As we have observed before, the primary materials of the chemistry of oil and coal become exhausted and do not renew themselves. If from the point of view of energy several solutions are envisaged, nothing permits us to assert that photosynthetic activity will take the place of basic processes.

(2) *Light chemurgy* is a field which makes even more calls upon new discoveries. Let us recall, as an example, the fact that although the chemistry of sugar has fallen below our expectations, it is none the less true that we foresee the manufacture of textile fibres from sugar. Mutations brought about by radioactive elements, hybridization, and selection allow us to place the vegetable kingdom in the forefront of research in chemurgy.

In conclusion, one must recall the role which the imagination plays in scientific progress. This is particularly true in the field which we have been discussing. We are bound to ask whether the most clear-minded of men should not devote great effort towards solving the problems which will arise when fossil deposits become exhausted; for the benefit of mankind, we must not allow our ideas to triumph only when 'the arable land of the world has been destroyed without forethought in every continent'.¹ Surely there is still time to put the vegetable kingdom at the service of mankind.

The trees and forests

Roger BLAIS

If the tree, whose roots penetrate into the soil, whose branches reach to the sky, is a chosen symbol of enduring life in so many religions, it is because wood allows man to make his fire burn, and to build and manufacture.

The cambium layer,¹ is the physiological marvel responsible for the gradual expansion of the ligneous frame. In our climate, the activity of cambium ceases in winter, and so growth is the result of the addition of a layer of wood each growing season. The thickness differs in different species and depends on ecological conditions (climate, soil, and the rival activities of neighbouring plants); it would be in the nature of a millimetre in a spruce of the high Jura and can reach as much as 20 mm in a poplar planted in a flat, fertile country. The rings, visible in a transverse section of a tree, record the annual variations in pluviometry, so that the study of such rings in trees a thousand years old throws considerable light on the climatic cycles of the past. This study is known as dendrochronology.²

The bulk of a tree is formed by all its annual growths. It is the same with the volume of wood in a given area of forest land. Variation takes on the shape of an S, but unlike other biological sizes, such as the height of a man, or many physical phenomena, there is no limit, no saturation point: a two-thousand-year-old sequoia or a lime tree over a hundred years old increases in diameter however slightly, and continues to do so as long as it lives. Man, in a hurry, urged on by his needs and anxious to make use of wood (*lignum* or *materia*³), does not wait for the death of a tree to put it to use. He fells saplings when they are thirty years old, *Pinus pinaster* when it is sixty, the fir tree when it is a hundred and twenty, the oak when it is a hundred and eighty or even two hundred years old, to obtain sawn timber of the best quality. Beyond these time limits, the preservation of capital in timber would not be econo-

mic, and man does not exceed them, except when the use of tree or forest is of a different kind: use as an ornament or as a protection against soil erosion in mountainous country, or for scientific reasons. Such is notably the case with biological reserves, one of the most attractive aspects of nature conservation.

Two large groups of trees

It is a mistake from the botanical point of view to speak of wood as a simple substance. Wood is a fibre whose texture ensures the maintenance and flow of crude sap; there are as many species of wood as there are different anatomical structures in trees. Trees are divided botanically into two large groups: the conifers in existence since the Carboniferous period, and the deciduous leaf-bearing trees (dicotyledonous Angiosperms) which appeared in the Cretaceous period. In the former, the wood is formed of a unique type of cell which carries out the two functions: the tracheid.⁴ In the deciduous trees there is specialization: unbroken vessels ensure the flow of sap and fibres ensure support. Tracheids, vessels and fibres are lengthened cells along the axis of the wood; we must add to these some horizontal component units of parenchyma⁵ which form the ligneous rays and subordinate parenchymatous or secretory components.

The shape of all these components, their dimensions, the nature of the 'bordered pits' (see note 4) within their linings, and their arrangement in relation to each other, differ not only within the two big groups, but between species to the extent that the structure of the wood of a given species is characteristic. A specialist can identify these differences from a small sample, much as a flower-lover can

(1) Cambium layer, Cambium: tissue which produces increased thickness of plant stems.

(2) Dendrochronology: from the Greek dendron, a tree; measurement of time by the study of trees.

(3) In Latin *lignum* denotes wood considered suitable for burning, and *materia* wood for building.

(4) Tracheid: a cell that is lengthened like a vessel and which functions as such. The sap flows from one tracheid to another by a special device known as 'bordered pits'.

(5) Parenchyma: cellular tissue, only slightly differentiated, which often, as in the case of wood, functions as reserve tissue.

(6) Lignin: a chemical substance which permeates the elements of wood and gives it its characteristic firmness.



Fig. 1. A wood of *Pinus sylvestris* in France in winter. (Photo Lod).

identify a leaf, a flower, or a fruit. There are also chemical, physical and mechanical differences which correspond with these structural divergences. Men who have made use of wood since pre-historic times—let us remember particularly the Magdalenians, who took part in the reconquest of the post-glacial tundra by afforestation—have known that different kinds of wood are suitable for different purposes, such as for making axe-handles, building huts, making ploughs and for the structure of cathedrals.

Cellulose

Let us consider these different properties, by making the chief sectors of use tally as accurately as possible, and by disregarding the chronology of the development of these sectors. The percentage composition of a piece of wood is as follows: carbon 50 per cent; hydrogen 6 per cent; oxygen 42 per cent; nitrogen 1 per cent; mineral matter 1 per cent. A kilogram of dry wood in the open air, that is to say with about 20 per cent humidity, gives off in burning 3,200 to 3,500 'large' calories. These facts explain the traditional use of wood as a source of heat in the house or factory; for the technique of carbonization, which gives charcoal; for the process of distilling wood in a sealed receptacle which in relation to the preceding technique and in addition to coal, enables us to collect and condense methyl alcohol, acetic acid and tars. They also explain why it is possible to convert wood or charcoal into gas in gas generators.

The molecular composition of wood is as follows: cellulose 40 to 60 per cent, hemicelluloses, polysaccharides, pectins, lignin 20 to 26 per cent and various other bodies (oily resins, tannins, colouring matter, mineral salts). A whole group of industries use cellulose. After the elimination of lignin,⁶ it is a question of obtaining a pulp in which the cellular fibres remain in good condition. The best solution of the problem involves processes using soda, sulphate or bisulphite, which result in rendering lignum soluble and releasing the fibres. This is the basis of the paper industry, which traditionally used rags, but was revolutionized after 1850 by the use of resinous woods with long fibres, especially spruce. At the start, this development had little effect on western forestry, factories drawing mostly on the immense reserves of conifers in the forests of the north. But economic conditions have altered. The afforestation policy of the states of western Europe is today turned largely to the production of wood for paper-making by the

growing of a large number of resinous trees, the conversion of other plantations to their growth and by reafforestation. Efforts are also being made throughout the world to use deciduous woods, whose fibres are shorter and of which the return is less, but whose production is in excess.

Cellulose, the principal ingredient of paper in which one finds the fibre in its natural state, is also the main ingredient of a whole group of industries which use it by breaking up its molecular chains (a process which gives rayon, fibran and cellulose films); by combining it with acetic acid to obtain acetates and powder used in casting and varnishing; or, after nitration, for the purpose of making celluloid, lacquers, photographic films, and explosives. Here we come across an important off-shoot of the chemistry of high polymers. As for lignin, it is a whole element in itself of the chemistry of wood which has still to be investigated thoroughly; it has as yet given uses of only secondary importance.

Constructive uses

Physical qualities—density, toughness, colour, and resistance to various forms of friction—are behind all the traditional uses of wood for household utensils and agricultural implements, in making casks, for crating and packing, carpentry, joinery, flooring, furniture, railway sleepers, telegraph poles and pit-props. Wood is used fresh, that is to say in its natural form without any treatment with preservatives, for pit-props; or after anti-cryptogamic treatment, for sleepers; or, after the old method of splitting, for casks; or more often, when pieces are needed for carpentry, for beams or boards, by mechanical sawing. There are also the processes of peeling, by which shavings are obtained for use as light packing material, and of cutting in thin sheets for use as veneers.

The choice of wood, the form in which it is supplied, the technology of construction and finish are in direct relationship to its use. Many crafts, such as carpentry, depend on skill in assembling and woodwork (joinery); for wood is anisotropic by reason of its structure and hygroscopic owing to its composition, with the result that its dimensions are liable to change more or less with its water-content, which in turn changes with the water-content of the air. Craftsmen have long known how to overcome the difficulties caused by the composition of their material, as we know from the roofed bridges and buildings dating back to the Middle Ages and from furniture

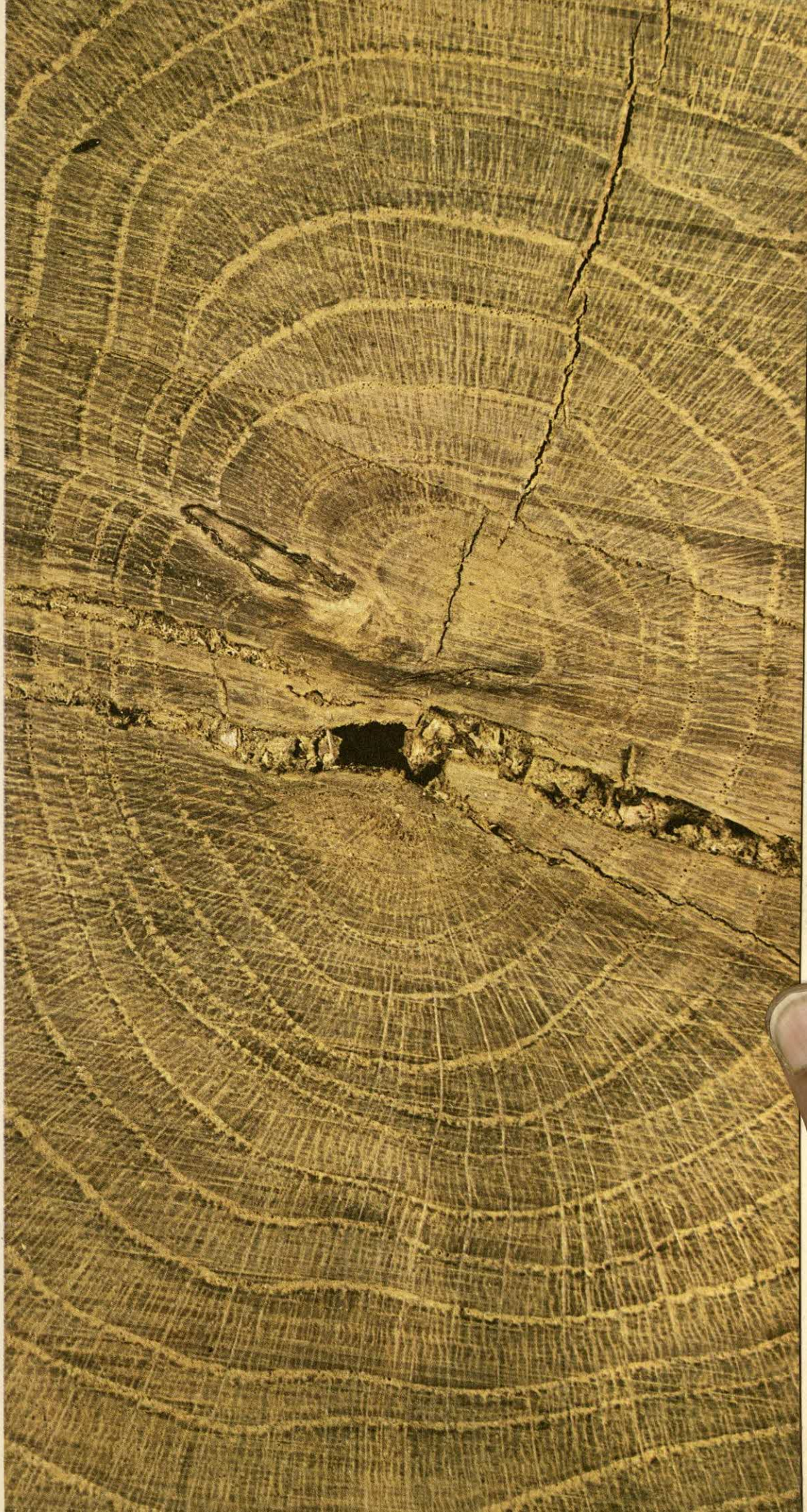
Fig. 2. Wood is made by the periodic activity of the cambium in woody plants, as the concentric rings in the transverse section of this walnut tree show. (Photo Lod).

several centuries old. By applying the principles of resistance of materials it has been possible to make appreciable progress. Nevertheless, wood competes nowadays with new materials, such as cement, iron and plastics, the homogeneous products of industry which make mass production and prefabrication possible. This is why manufacturers using wood have been induced to make from their material half-finished products of standard dimensions that are not liable to shrinkage. This would not have been possible but for the progress made in the chemistry of adhesives, the strong glue used by the old cabinet-makers having given way to adhesives of animal origin such as casein and synthetic resins (phenoformal, urea-formal). Lignin itself can, in a certain technique, once it has been reactivated, play the same part as the large molecules of synthetic resin.

Laminated boards, such as plywood, are made by superimposing and gluing under pressure sheets of wood whose grains are placed at right angles. A related process has made possible the production of the directly prefabricated units used in building, especially flat-surfaced doors. Bakelite, a material of exceptional quality, is also obtained from resins; it is outstanding for insulation in electricity. By using the technique involved in making plywood, it is possible to replace veneers by boards and as a result to make constructions of a size and shape which it would be impossible to make out of solid wood.

The manufacture of plywood necessitates the use of wood of special quality; by shredding inferior wood, by using waste wood or shavings and reconstructing them with adhesives, it is possible to make boards whose use in building and furniture-making will eventually increase to such an extent that they will compete seriously with plywood. By removing the fibre of wood, using techniques allied to those employed in the pulp industry, fibrous sheets are made whose range of use is also extensive.

Whether *lignum* or *materia*, in an astonishing variety, wood is constantly renewed in the depths of the forest. Wood is one of man's staunchest allies, especially where his future is concerned. What prospective value must we not attribute to the worship of the ash 'Yggdrasil' by the Scandinavians, the oak by the ancient Greeks and Gauls, and the 'acvattha' by the Hindus?



Plants and health

Jean-Paul TISCHMACHER

(1) The best-known 'electuary' is theriac, whose popularity lasted for three centuries.

(2) The first alkaloid was isolated by Sertüner in 1817: it was morphia. A little later Pelletier and Caventou discovered quinine, Runge caffen, and Tanret pelletierin. Other discoveries following in succession, doctors had at their disposal an enormous number of highly active products (of which the best known are atropin, cocaine, nicotine, pilocarpine, papaverine, sparteine, strychnine, etc.). Among the more recent is reserpine, which is well-known in

Continued on next page

The use of plants in preventing disease or restoring health dates back to very ancient times. As early as 1500 BC, we find stylized medicinal plants carved in relief or in intaglio on the walls of the temple at Karnak in Egypt and on Assyrian, Sumerian and ancient Persian buildings.

One of the most accurate likenesses of a medicinal plant is that of sylphium on the coins of Cyrene, between 800 and 200 BC. This umbelliferous plant of the genus *Ferula* was used so extensively as a medicine by the ancient Greeks and Romans that at the beginning of the Roman Empire it died out. It was sold for its weight in gold in the markets of Athens and Rome and was used, according to Hippocrates, both as a sudorific and to reduce fevers. History records only one sample, and the last known of this drug—that presented with great pomp to Nero.

The Bible, The Rig-Vedas, The Iliad, The Odyssey and The History of Herodotus give much information, brief but to the point, about the medicinal uses of a great variety of plants. Writers who specialized in medicine (Hippocrates, Dioscorides, Galen, Pliny, Scribonius, Largo, Celsus, etc.) were no longer content merely with enumerating and describing medicinal plants; they specified definite forms of use and gave the most complex descriptions for the preparation of medicines, mostly with a basis of powdered plants (for tonics, ointments, etc.). The age of medicine had arrived.

Powders, dyes and extracts

Under the influence of the old Arab school of medicine, three doctors, the German Cordus, the Spanish Monardes and the Frenchman Charles de l'Ecluse (Clusius) devised prescriptions that became more and more complex. Their aim was to find a panacea or medicine which was quickly to cure all known and unknown illnesses, and

they produced curious formulas which contained one hundred different ingredients. Most of these were of vegetable origin, though they also included pulverized viper and lizard, and a number of powders, minerals and salts. The resulting substance was mixed with honey and spices to make a thick paste or 'electuary'.¹ The moulding of this paste into separate little spherical masses gave pills the form which is so well known in pharmacy.

Meanwhile, other scientists sought to simplify all this jumble and tried to concentrate the activity of plants to obtain more active medicines or those that were free from side effects. It is thus that *dyes* came into being. These were obtained by the maceration of plants in a solution of 10 or 20 per cent alcohol. *Essences* are produced by concentrating and evaporating dyes; in this process the active and soluble constituents of 10 or 20 gm of plants are reduced to 3 or 4 gm of a thick or dry product.

Other scientists sought to reach the same results through distilling. It was in this way that the first isolated active constituent of a plant was discovered: 'flowers of benzoin', the acid nature of which was soon realized. It was almost pure benzoic acid.

In proportion as chemical and analytical methods were perfected, so the discoveries of active constituents increased boundlessly. It was soon realized that the active constituents of drugs are chemical compounds; important factories and laboratories were set up to extract or make such chemical products. Two large groups of organic compounds extracted



Fig. 1. Sylphium was much valued in ancient times, as is shown by these Cyrene coins on which it is depicted. The species is now extinct. (Bibliothèque Nationale, Paris. Photo Lod).

from plants are particularly important: the alkaloids and the glucosides.

The alkaloids, although often strong poisons, have remarkable therapeutic properties. Their complex and very varied chemical composition has a typical common feature: the regular presence of nitrogen in their formula, which gives them a basic characteristic; hence the term vegetable alkali, which was their original name.²

The glucosides have the quality in common of dividing under the action of fermenting agents and giving a molecule of glucose and another compound of very variable composition as the case may be. The heart-stimulating qualities of digitalis (digitalin, digitoxin, digitanid, digoxin) and of the Apocynaceae (oleandrine, thevetine), the saponins and the laxative properties of the aloes all come into this group.³

A normal compound of the extract of various crucifers, the extract of mustard (allyl-isothiocyanate) is used chiefly as a counter-irritant. It has only recently been discovered that this substance possesses the property of acting on the mitosis of the cells and may be capable of causing genetic mutations. Perhaps some day this compound (or one of its derivatives) will become a weapon against cancer.

Vitamins and antibiotics

The vegetable kingdom is an important source of vitamins which are important in keeping man in good health. Vitamins C, D, B₁, E and K are extracts of vegetables or of yeast. Vitamin B₁₂, an anti-anaemic agent, discovered in 1948 in the liver from which its extraction is very difficult, is now made from cultures of *Streptomyces griseus* as a by-product of streptomycin.

Antibiotics have the peculiar quality of preventing the development of pathogenic bacteria. They are usually extracted from cultures of lower fungi. Since 1939, when the first of them, penicillin, was discovered by Fleming, many other antibiotics have been isolated: chloramphenicol (tifomycin), erythromycin, streptomycin, tyrothricin, viomycin, etc. Their use has to a great extent lengthened the average span of human life, and made it possible for surgeons to succeed in operations which only fifteen or twenty years ago were extremely risky.

The contribution made by plants goes even further; research into the nature of the active constituents which they contain has given a direct stimulus to the scope of chemistry. Many simple substances formerly

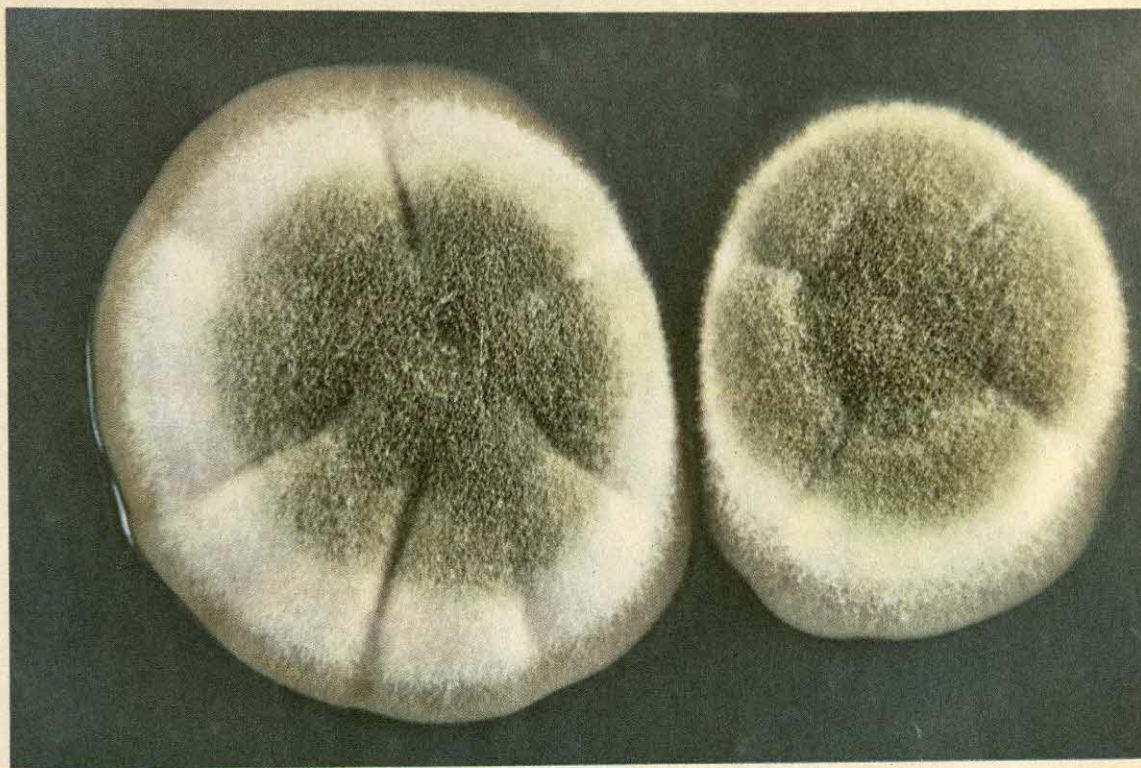


Fig. 2. In the widest sense of the term, we can include moulds among plants which are valuable for the health of man: such are the cultures of *Penicillium notatum*, which produce penicillin. (Culture Société industrielle pour la Fabrication des Antibiotiques, Paris. Photo Lod).

extracted from plants are now fully synthesized in the laboratory. Chemical research concerned with providing drugs which give more active results, and which are less toxic, has been directed, often with success, to transforming constituents of vegetable derivation into new products with extremely interesting qualities. When methylated, morphia gives codeine, well known as a cough medicine, which is distinctly less toxic than morphia and does not have the grave disadvantage of being habit-forming.

While experimenting in the production of synthetic cocaine, chemists have discovered chemical substances of simpler formulae, with greater powers as anaesthetics, but three to ten times less toxic (novocaine, pantocaine, etc.). Even some antibiotics are now made synthetically, which results in an appreciable lowering of their cost.

To sum up, plants not only cure man's ills through their contents or through what is extracted from them; they also urge him to further research which will allow him to overcome, if not death, at least illness.

Continued from previous page

the treatment of high blood pressure and some nervous diseases. Again, quite recently, a fungus used by Mexican Indians in their religious rites has been brought back and isolated by Professor Roger Heim. From this has been isolated psilocybine, a substance with psychotherapeutic properties which seem to suggest that it has a brilliant medical future.

(3) Innumerable other chemical compounds are provided by plants: alcohols (ethyl alcohol, a disinfectant; octylic alcohol, a hypotensor); poly-alcohols (glycerine); more or less complex acids (tartaric, citric, malic, agaric acids and santonin); fatty acids, amongst which are chaulmogric, hydrocarpic and gorlic acids, which were the first drugs used against leprosy; ketones, aldehydes, phenols, terpenes (menthol, camphor, borneol, thymol, etc.). A well-known plant derivative, absorbent cottonwool (which is almost pure cellulose) though not strictly speaking a medicine, is of prime importance in surgery; indeed one can certainly not imagine carrying out any operation without it nowadays.

Plant beauty

Yotaro TSUKAMOTO

Number of varieties of
garden plants
(after Emswiler, 1937)

Rose	15,000
Chrysanthemum	1,500
Narcissus	3,000
Tulip	8,000
Sweet pea	500
Antirrhinum	400
Aster	600
Dahlia	7,000
Gladiolus	2,500
Iris	4,000
Peony	2,000

The origin of horticulture is uncertain, but it is thought to be an art as old as human history. Archaeological excavations give us some idea of the varieties of flowers which decorated the gardens of Egypt and Mesopotamia. For example, the water-lily, which grows naturally on the Nile, was well known to the Egyptians. In those days communication between distant countries was rare, but, later on, migrating peoples took garden plants with them on their wanderings. In this way the Saracens introduced *Iris albicans* into all the countries they penetrated, and the Roman legions took the Madonna lily from southern to northern Europe. It was probably used medicinally and was planted near their camps for this purpose.

After the establishment of the modern states of England, France and Holland, many wild and cultivated plants were introduced into Europe from South Africa, Asia, North and South America, and contributed to the variety of garden plants in the Old World. *Rosa sinensis* and *Dianthus sinensis* deserve special mention, for they provided the stocks from which we derive, respectively, modern roses and carnations.

These two particularly important flowers have been cultivated in the West since Roman times, but they are far from being the only ones. Numerous other Mediterranean bulbs and annuals were grown just as extensively.

In fact, until modern times, the Mediterranean countries provided all the main plants in European gardens. We have only to look at some of the seventeenth-century books on garden plants to see that this was so.

Apart from the natural landscape style prevalent in English gardens, the plan of European gardens from Roman times up to the present day was strictly geometrical. This was in strong contrast with the design of Asian gardens, especially those of Japan, where the gardens were laid out with a dynamic symmetry.

A brief survey of the garden plants of Asia shows us that, whereas those of Europe originated in the south, those of Asia came from the north, that is from north-west China. For their gardens the people of these regions selected flowering trees and perennial plants, such as the tree peony, flowering peach, peony and chrysanthemum, which they cultivated either in beds or in pots.

Like the Chinese, the Japanese gave pride of place to ornamental trees and although they introduced a great number of garden plants from China, they also bred plants indigenous to south-west Japan, such as azaleas and camellias, so that by the seventeenth century there were numerous Japanese varieties of azalea, camellia and tree peony. For some time now, taxonomists have thought that Japanese gardeners must have got these azaleas and

Fig. 1. The rose, messenger of beauty, has remained the symbol of one kind of formal perfection: hence it appears that there are aesthetic rhythms within nature, and that plants are the clearest evidence. (Photo Lod).

camellias by selecting from the natural hybrids which occur in wild populations and contain different types within the same species.

By the end of the seventeenth century, modern cities had developed in Europe and Asia, and their inhabitants wanted flowers to brighten their homes. This need led to the development of pot flowers and, later, to cut flowers. The latter, especially, are now an industrial product in the United States, where vernalization and photoperiodic techniques enable them to be produced all the year round.

Floral decoration has also become an art. Originally the difference between the floral art of Japan and that of Europe was as great as the difference between the styles of their gardens. But this difference is fast disappearing as a result of closer communication between the two hemispheres, and now a modern floral art is developing which makes use of non-floral materials, such as wood, metals and plastics.

Another world-wide trend is that gardeners are using more and more plants of all sorts, annuals, bulbs, perennials and shrubs, to fill flower-beds and make green borders along streets.

For all this we are indebted to the extensive labours of the flower growers, who have given so many varieties to the gardens of the world. Perhaps the most famous name is that of Pernet Duchet, who created the yellow rose called *Pernetiana*. Today there are many excellent rose cultivators, who confront us with new varieties every year. The speed at which the garden varieties are increasing is shown in the table, which gives the number of varieties of the more popular flowering plants in 1937. Today the numbers are much greater and there are some 2-3,000 more varieties of roses and dahlias, and the varieties of chrysanthemums and gladioli have doubled.

However, progress has been made not only in quantity but in quality. The carnation, the gladiolus, the petunia, the rose and the tulip, have all been remarkably improved since the second world war. The same is true of the popular annuals, such as the pansy and the daisy, which have both been improved from the wild strains of Europe. Doubtless we can expect even greater achievements in the future.



The future of plants

James BONNER

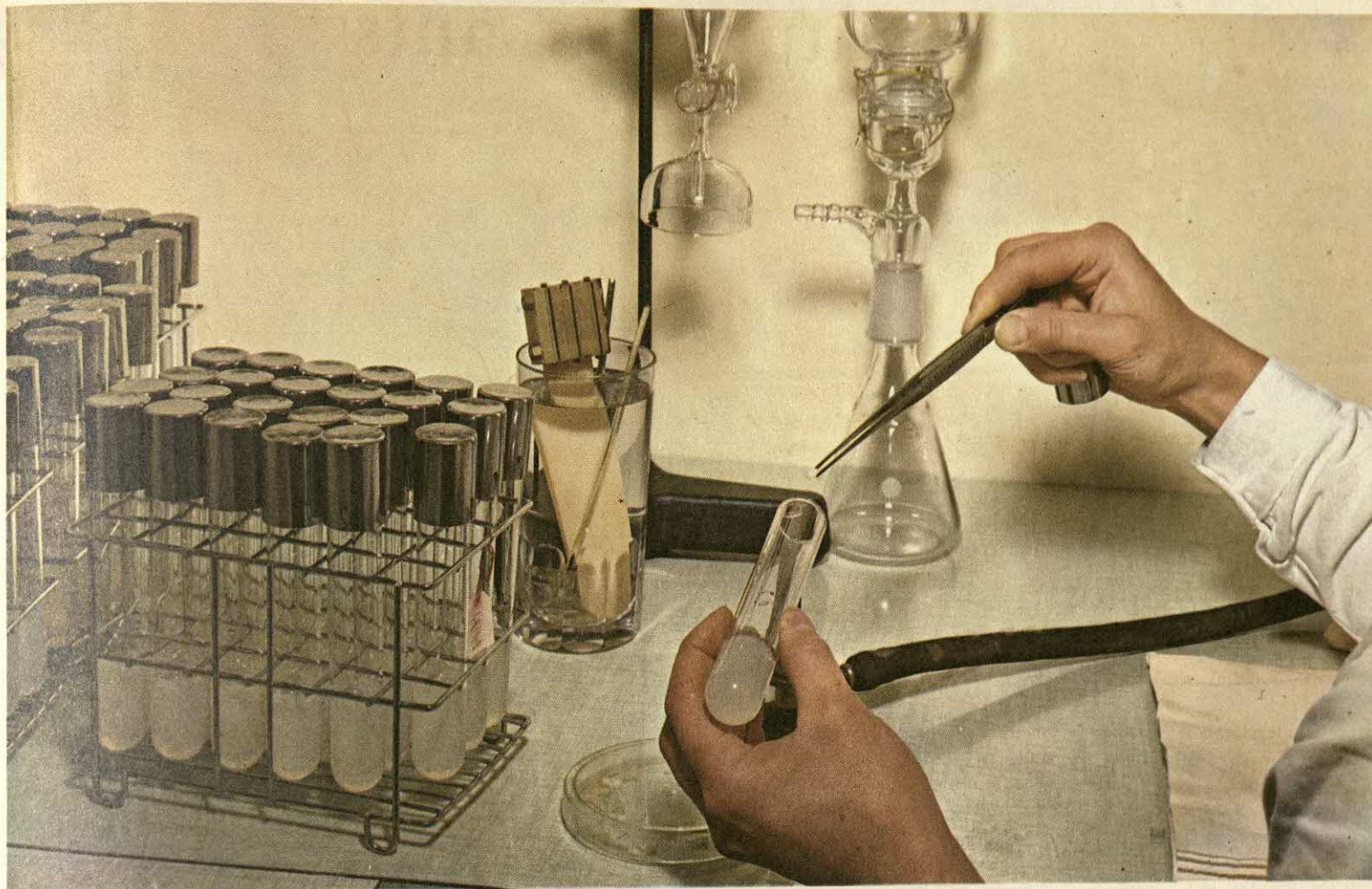
We are accustomed in our rapidly changing industrial society to the concept of obsolescence. Something is invented, produced, and used, only to become obsolete because it has been replaced by something better. There is, however, little prospect that plants will follow this pathway to oblivion. When we look into the future, even the distant future, it seems quite clear that people will continue to eat food and will continue to breathe oxygen, and these commodities are the two great gifts of plants to man. Our world has changed dramatically and will continue to do so for long into the future, but in the midst of all this change the dramatic thing about food is that it changes and can change so little. People must supply themselves with energy and with chemical building blocks for growth, by eating the enormous variety and complexity of chemical substances which we know as food, and which are the very chemical substances which are synthesized by the green plant. People breathe oxygen and give off carbon dioxide and it is again the green plant which recycles carbon dioxide, producing the oxygen which is required for our human sustenance.

The main problem about the world's food supply is that it is not sufficient. This is because the number of human beings in the world is increasing and has increased rapidly in years gone by. Although at the present time the world is increasing its food supply at a rate sufficient to maintain the *per capita status quo*, this has not been true in the past, and for a long period of time growth of the human race outstripped increase in food supply. As a result, over half of the people of the world today are hungry and undernourished. There is of course an upper limit on the amount of food which can be produced on earth and hence an upper limit on the number of people who can be fed. But in principle it should be possible to produce food for several times as many people as

there are present on the earth's surface today. To do so will require an agriculture which is much more intensive than today's. Let us discuss some of the factors which determine the number of people who can be fed by plants grown on the earth's surface.

Japan's example

Although a very great amount of plant material is formed each year by photosynthesis over the earth as a whole, human beings confine themselves almost completely to eating the produce of their cultivated plants and this constitutes but a small fraction of the total. We use the oceans with low efficiency. We do not eat trees. We eat cultivated plants or animals which feed on cultivated plants. The cultivation of plants, although it is a very old art, is not in general practised with any great efficiency. The Japanese, for example, who have the world's most intensive agriculture, produce almost four times as much food per acre as does the average farmer of the world. The Japanese produce a great deal of food per acre because they not only have the technical know-how of modern science, making high production possible, but they also have a high population density which makes it necessary for them to use their technology at a high level of intensity. It is clear that if the techniques of modern agriculture as practised in modern Japan or in western Europe were to be spread to all of the earth's acres, at present cultivated, we could feed adequately a great many more people than are fed inadequately today. Our advances in agricultural technology should also make it possible to increase somewhat the number of cultivated acres on the earth's surface and to spread agriculture into the wet rainy regions of the tropics and northward into the cold wet areas of the temperate zone. And it is by the worldwide spread of modern intensive agricultural technology and the increase to its ultimate limit of the number of cultivated



acres on the earth's surface that it should be possible eventually to feed a world human population three or four times the present one—a population of perhaps 9 billion human beings. And this is the population which demographers tell us we must foresee for the world within 100 years or even perhaps slightly sooner.

To approach this high level of productivity of food will take a long time. The diffusion of agricultural knowledge to underdeveloped areas is a slow process. Many people must be educated; factories must be built to make fertilizers, insecticides and so on; research institutes must be founded to breed better plants and animals; dams, canals and other engineering works must be made; transportation facilities must be provided. In general the technological advancement of agriculture goes hand in hand with industrial development. And because this is so it has proved impossible in the past to increase agricultural productivity at a rate of more than a few per cent per year. This rate of increase, although it will provide food for the increasing number of human beings in the world, will

not suffice to increase their standard of living. We can reasonably hope to increase the standard of living of people and supply them with more and better food only as the rate of growth of the world's population decreases, and only as the world population tends towards ultimate stabilization.

The use of seas, deserts and forests

There are many things which we might do to provide food for human beings in addition to improving conventional agriculture. For one thing we might learn how to use the sea more efficiently. Although a great deal of photosynthesis takes place in the waters of the ocean, we have so far profited little by it. One of the things that we might do in our efforts to use the ocean is to look into the possibility of domesticating sea-going herbivorous animals—animals which would graze upon the floating algae of the ocean just as cattle graze upon the grass of the land surface. Then, too, we might introduce into cultivation portions of the vast desert area of

Fig. 1. A laboratory in the phytotron at Gif-sur-Yvette, showing the sowing of culture media in tubes. The laboratory culture of plants will be very important in the future. (Photo Lod).

the world. The earth's deserts amount in area to perhaps twice the area of the cultivated land. The irrigation of deserts requires a new source of fresh water and this means of course the reclamation of ocean water. Agriculture carried on with reclaimed ocean water, although it will be expensive, is nevertheless a real possibility and one which we must foresee for the long-range future.

The forests, which include almost one-half of the total plant material produced by photosynthesis each year on the earth's land surface, will have their own role to play in the future of our more and more intensively populated planet. One can calculate, for example, that at the present rate of increase in the use of paper for books and for newspapers and for private correspondence, it will soon demand all of the produce of all of the earth's forests to supply the requisite amount of paper, and this in the space of a mere three or four generations. But the forests must supply us with other things as well. As our petroleum supplies become depleted and as coal and other fossil fuels become harder to obtain, forests will remain our last generally available reservoir of reduced chemical compounds—compounds which we shall be able to use in chemical industry as the basis for making medicines, synthetic vitamins, plastics, and so on.

The future of plants

And so when we look into the very long-range future of plants, we see that plants will necessarily be with us. We shall have extended our cultivated areas; deserts will be irrigated with water purified from the ocean; loss of crops to pests, which is at present very significant, will be abolished. In our agriculture of the future we shall undoubtedly cultivate new plants created by modern genetics and particularly rich in the materials which the human diet requires. Thus we shall have plants rich in edible fat or rich in edible protein. But aside from this, plants will, like people, remain much the same. Human beings, although they will perhaps not change very rapidly, will certainly change in eating habits. As the world becomes more crowded with people we shall become increasingly vegetarian. As the mass of human flesh on earth increases, the mass of animal flesh will inexorably decrease. But our vegetarian diet will be a wholly satisfactory one, nutritious and attractive. It will contain synthetic vitamins and amino acids, so that each mouthful will provide a complete and

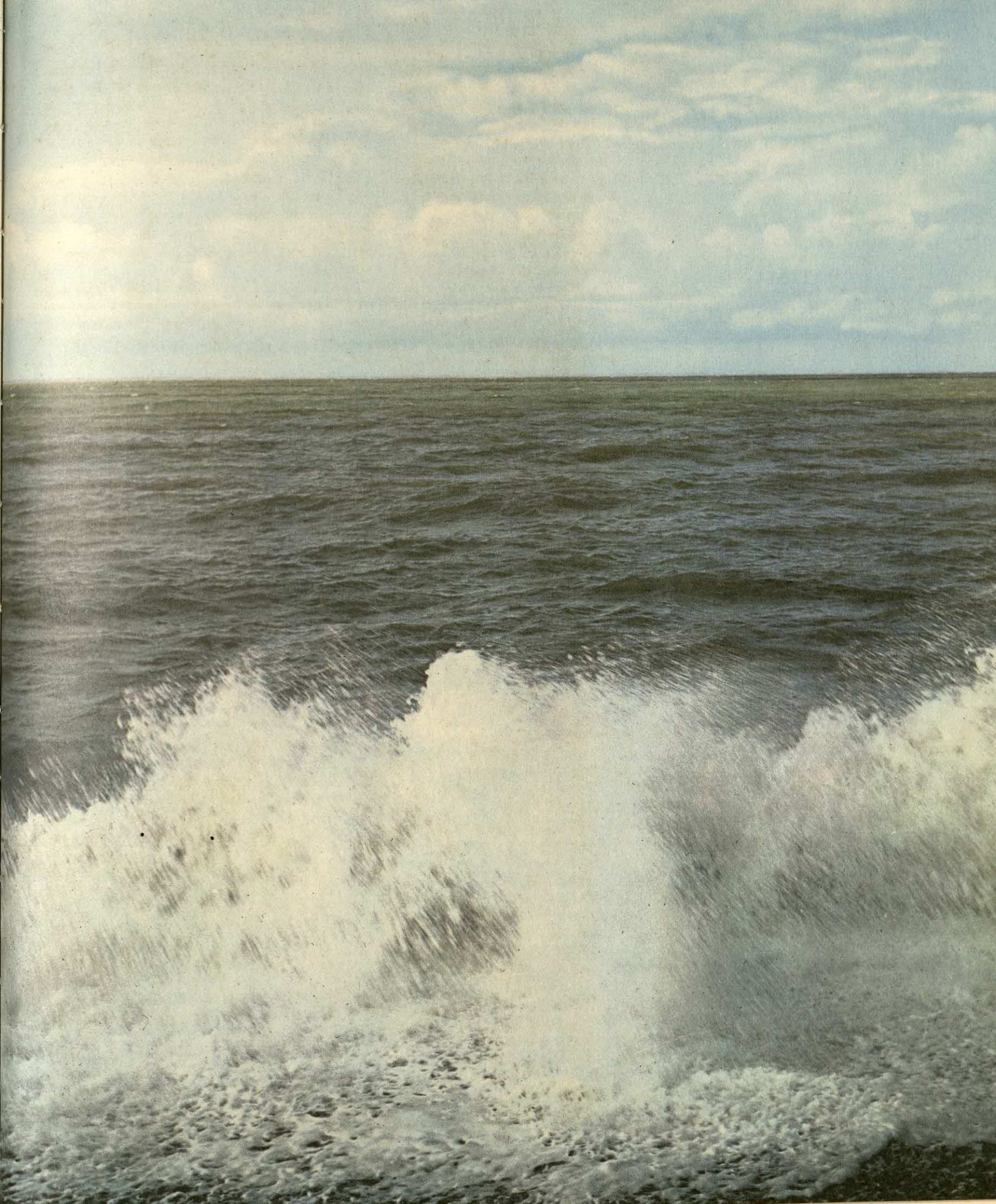
balanced unit of nutrition. It will contain flavouring materials reminiscent of the days when man wastefully fed a portion of his produce to animals, recovering the materials thus squandered, in low yield to be sure, as products suitable for the human diet.

And as today, the process of photosynthesis will daily renew the atmosphere of our planet, extracting the carbon dioxide given off by man and by his works, and replenishing the oxygen upon which we all depend.

Thus, the future role of plants in our industrial technological society is secure. Indeed there will be an ever-increasing amount of work for our cultivated plants to do; more and more human mouths to feed. But to accomplish the task of supplying all the peoples of tomorrow's world with food, it is necessary that a great deal of work be done today. We must for one thing take all the steps needed to ensure that modern knowledge of plant science is distributed to all the world's peoples, so that they can participate fully in increasing the world's food supply. For another thing we must intensify research on many aspects of basic plant science. We must for example have knowledge of how to produce suitable crop plants for cold regions or hot regions; how to cause plants to make flowers and fruits on demand rather than naturally; how to abolish disease and particularly the virus diseases which now exact such a toll of the world's produce. We could well discover how photosynthesis works. True, we know a great deal already about this most basic of life activities, but we do not yet really understand how the light absorbed by the green chlorophyll of the plant cell is transmuted into chemical action. When we do understand this elementary act we may very well find that we can do something about it, perhaps make it more efficient. Then, too, many new kinds of plants remain to be discovered. It is estimated that only two-thirds of all species of plants have thus far been collected and described; the remainder await the plant explorers of the future. And who knows, perhaps these plants—still to be found—will provide us with new crop plants, crops more appropriate to our industrialized society than those introduced by our forefathers 7,000 years ago and which we still use and cherish today.

Plants then will always be with us: their use in the maximum effective and productive ways will be a challenge to plant science far into the future.

Fig. 2. In the future shall we be able to create a thriving plant life on the vast expanse of the oceans? (Photo Lod).



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